

Hydrological Conditions Regulate Dissolved Organic Matter Composition and Molecular Weight in the Aquatic Continuum of a Large Freshwater Lake on the Qinghai-Tibet Plateau

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Abstract

River and lake ecosystems in alpine environments are extremely sensitive to climate change and act as hotspots in the global carbon cycle—particularly in regions characterized by a rapid hydrological cycle. Dissolved organic matter (DOM) constitutes the largest organic carbon pool in aquatic systems; however, research on DOM variation and its response to hydrological conditions along the river–lake aquatic continuum in the alpine freshwater ecosystems remains limited. In this study, water samples were systematically collected from multiple sections along the aquatic continuum of Lake Cuona, a typical glacier-fed freshwater lake at high-altitude region (around 4,650 m a.s.l.). A combination of optical spectroscopy, ultrahigh-resolution mass spectrometry, high-performance liquid chromatography, and stable water isotopes (i.e., $\delta\text{D-H}_2\text{O}$ and $\delta^{18}\text{O-H}_2\text{O}$) measurements was applied. We found rapid turnovers of DOC concentration, DOM molecular weight and their compositions along the continuum. FT-ICR MS and optical analyses confirm that DOM shifts from a terrestrially derived pool to one with greater microbial or algal production as water moves from upper rivers to downstream reaches. Significant relationships between the DOM characteristics and water isotopes were observed, suggesting the contribution of hydrological conditions in modulating DOM compositions. Interestingly, changes in DOM composition exhibit a stronger response to hydrological conditions in lakes predominantly governed by natural processes than in rivers primarily influenced by anthropogenic factors. These findings demonstrate that alpine lakes and rivers on the Tibetan Plateau could play a prominent role in regional and global carbon cycles under future climate change scenarios, particularly when considering projected shifts in hydrological conditions.

1 Introduction

River and lake ecosystems in remote alpine areas are extremely sensitive to global climate change, especially to the impact of glacier melt and permafrost thaw on the downstream aquatic ecosystems (Singer et al., 2012; Spencer et al., 2014; Zhou et al., 2023). The carbon (C) cycle in river and lake ecosystems plays a key role in carbon budget at regional and global scale (Tranvik et al., 2018). In these aquatic environments, dissolved organic matter (DOM) constitutes the predominant species of organic carbon (Cory et al., 2018), though its bioavailability and photoreactivity covaries with its source and composition (Kothawala et al., 2014; Kellerman et al., 2014). DOM serves as a bridge connecting terrestrial-aquatic organic matter from the glaciers, permafrost, river and lake ecosystem, exhibiting pronounced seasonality in composition and properties (Maurischat et al., 2022). DOM is considered an essential factor in modulating water quality and ecosystem functions (Hu et al., 2016; Shang et al., 2018). The DOM reactivity, including its bioavailability, the transfer pathways in aquatic food chains, participating in nutrient cycling and the associated alterations in water optical properties, collectively serves as a major driver of aquatic ecosystem processes (Stadler et al., 2020; Cory et al., 2014).

As a critical aquatic continuum, aquatic ecosystems are simultaneously regulated by allochthonous DOM (e.g., surface runoff, precipitation, and human activity discharge) and autochthonous DOM (e.g., phytoplankton and microbial metabolites). The DOM characteristics in aquatic environment is extremely

affected by both natural processes and external disturbances, thus showing substantial temporal-spatial heterogeneity (Song et al., 2019). Many studies have revealed that climatic factors, hydrological connectivity, and natural processes in alpine ecosystems with bare vegetation and limited human activities can influence DOM amounts and properties (Ishii et al., 2012; Kellerman et al., 2014; Sepp et al., 2019; Du et al., 2021; Woolway et al., 2020). From upstream to down-stream aquatic systems along hydrological pathway, DOM could be processed and transformed via photodegradation, biodegradation, and adsorption/desorption at mineral interface, and thus resulting in attenuation of the terrestrial signals for aromatic compounds (Bowen et al., 2020; Massicotte et al., 2017). Along fluvial networks, the loss of DOM amount or alteration commonly occurs via mineralization, microbial transformation and photodegradation (Bittar et al., 2015; Bogard et al. 2016). However, this patterns can be changed by anthropogenic disturbances such as urbanization, agricultural land use, and pastoral activities (Ye et al., 2019; Zhou et al., 2021). The release of “old” organic matter from thawing glaciers and permafrost may exert a profound impact on carbon cycling in alpine river and lake ecosystem due to its high bioavailability and potential environmental effects (Spencer et al., 2014; Wang et al., 2018; Smith et al., 2018; Zhang et al., 2023). Nevertheless, mechanistic understanding of DOM transformation throughout the alpine aquatic continuum—especially in freshwater system of the remote Qinghai-Tibet Plateau (QTP) outflow regions—remains limited.

The QTP, known as the “water tower of Asia”, is a major water source for many large rivers, such as the Yangtze River, the Yellow River, and others. As one of the regions with the most concentrated glaciers and alpine lakes in the world, the Tibetan Plateau (TP) acts as a critical indicator of ecological environment and plays a vital role in maintaining global climate stability (Feng et al., 2016; 2024). Monitoring data in recent years have revealed that temperature on the TP is quickly increasing at a rate of approximately 0.03°C per year, which is about three times the rate of the average global warming (Sun et al., 2018; Thompson et al., 2000). Concurrently, the climate regime of the QTP has shifted towards significant warming and wetting, characterized by increased precipitation, reduced wind speed, and decreased evaporation. Previous studies have identified water residence time and temperature as key factors regulating dissolved organic matter properties in alpine lakes (Du et al., 2021; Sepp et al., 2019). A gradient of prolonged water retention time along hydrological pathways—from headwaters to downstream water—can stimulate DOM degradation, and subsequently change the DOM quantity and quality (Groeneveld et al., 2020). Water isotopes ($\delta\text{D-H}_2\text{O}$ and $\delta^{18}\text{O-H}_2\text{O}$) serve as effective hydrological tracer for identifying water sources and evaporation processes at the catchment scale (Fellman et al., 2020). Lakes with longer water residence times typically exhibit more enriched $\delta\text{D-H}_2\text{O}$ and $\delta^{18}\text{O}$ values (Kellerman et al., 2019; Johnston et al., 2020).

However, prior studies on aquatic continuum DOM mostly concentrated on low-altitude inland lakes (Sankar et al., 2020; Sepp et al., 2019) with rare reports in alpine lake. Cuona Lake, the source of Nujiang River and one of the highest-altitude freshwater lake globally, remains relatively pristine due to minimal anthropogenic activity. Recent observations indicated a rapid rise in water level and continuous expansion of surface area in Cuona Lake. Glacial meltwater, a major contributor to Cuona Lake, is

expected to introduce substantial amounts of legacy organic matter into the aquatic system. As a crucial link in the aquatic continuum connecting glacial meltwater from the Tanggula Mountains with the downstream Nagqu and Nujiang Rivers, the variation of DOM concentration and molecular composition in Cuona Lake will directly affect the carbon cycle in downstream freshwater ecosystems—especially in regions with rapid hydrological changes. Although recent work has documented responses of DOM molecular composition to hydrological conditions in both glacial-fed and non-glacial-fed rivers and lakes along the Selin Co watershed (Zhou et al., 2023), the attribution of surrounding rivers and lakes to the DOM pool in Cuona Lake remain poorly constrained. Moreover, the response of DOM in high-altitude freshwater lakes to climate change—particularly in terms of quantity, molecular weight, chemical composition, and its reactivity under varying hydrological conditions—is still not well understood. To better assess the impact of continuous warming on freshwater DOM on the QTP, it is crucial to clarify how DOM responds to hydrological changes throughout the aquatic continuum of Cuona Lake.

In our study, we focus on the glacial-fed, freshwater Cuona Lake to elucidate how the chemical diversity of dissolved organic matter (DOM) responds to multi-source recharge and covaries with hydrological conditions along the aquatic continuum of Cuona Lake. For this purpose, we conducted a comprehensive investigation of DOM variability by application of DOM concentration, optical measurement, ultra-high resolution fourier transform ion cyclotron resonance mass spectrometry (FT-ICR MS) and high performance liquid chromatography (HPLC) techniques. In addition, water stable isotopes and water chemistry were analyzed to reveal the hydrological and hydrochemical controls on molecular DOM diversity, ultimately clarifying how alpine freshwater DOM responds to climate change. We hypothesized that intense photodegradation (especially UV radiation), evaporation, and enhanced autochthonous production would result in decreased DOM aromaticity, molecular weight, and humic-like components along the flow path. Furthermore, we expected DOM composition would be strongly associated with variations in water stable isotopes. Identifying the distribution of dissolved organic carbon (DOC) and the relationship between DOM composition and hydrological conditions in high-altitude freshwater ecosystem is meaningful for understanding carbon cycling processes and DOM reactivity in downstream aquatic systems.

2 Material and Methods

2.1 Water Sampling

The Cuona Lake, located on the northern Qinghai-Tibet Plateau (31°55'~32°08' N, 91°25'~91°33' E), is a large freshwater lake on the QTP. A substantial volume of glacial meltwater from the southern slopes of the Tanggula Mountains flows into the lake and ultimately discharges into the Nujiang River.

Characterized by a fragile and unique ecosystem, Cuona Lake represents a typical alpine system for studying the impact of climate change on high-altitude freshwater ecosystems. The lake surface lies at an elevation of approximately 4,588 m, covering an area of 182.6 km² with an average depth of about 12.64 m (Ma et al., 2011). Multi-year observational data from the Amdo Meteorological Station indicate that the lake region has an annual average temperature of 1.4°C, with mean annual precipitation and

evaporation of 411 mm and 1,783 mm, respectively (Yin et al., 2013). Lake recharge is primarily supplied by surface runoff from four rivers: SangQu (SQ), Zhuogequgang (ZGQG), WanggaQu (WGQ) and BasoQu (BSQ). Lake water exits via Ganong Ma (GN), converges into the Nagqu River, and eventually flows into the Nuijiang River (Fig. 1).

Surface water samples were collected at a depth of 0.5 ~ 0.8 m in July 2024 during the wet season, a period representative of annual average hydrological conditions and characterized by high hydrological connectivity. The sampling campaign included Cuona Lake (CN), the inflow lake Cuoja (CJ), the outflow lake Ganong Ma (GN), and four major recharge rivers, collectively referred to as the Cuona continuum. A total of 13 river samples were obtained from SangQu (SQ), Zhuogeiqugang (ZGQG), WanggaQu (WGQ), BasoQu (BSQ), Nagqu (NQ), along with 35 lake samples covering Cuona, Cuoja, and Ganong Ma (Fig. 1). For evaluating the spatial distribution of DOM concentration and the relative contributions of different recharge sources to DOM pool of Cuona Lake, sampling sites within the lake were distributed throughout the entire lake and grouped into five regions: east (CN/E), south (CN/S), west (CN/W), north (CN/N) and center (CN/M). Lake samples were collected using a rubber boat to access offshore areas, with a minimum distance of 2 km maintained between adjacent sites in Cuona Lake. Unless otherwise specified, all water samples were stored at 4°C in the dark immediately after collection and subsequently 0.22 µm membranes filtered within 12 hours using brown polyethylene bottle. Filtrates for DOC concentration, optical characterization, HPLC-SEC, and FT-ICR MS analysis were stored at -20°C until further analysis.

2.2 DOC Concentration and DOM Optical Characterization

DOM concentration (expressed as DOC, mg L⁻¹) was measured by a total organic carbon analyzer (TOC-V, Shimadzu, Japan). Water quality parameters including pH, dissolved oxygen (DO), and total dissolved solids (TDS) were recorded in situ with a portable multi-parameter probe (IN-Situ, SMARTROLL MP, Japan). Prior to optical characterization, samples were filtered in the field through 0.22 µm polyvinylidene fluoride (PVDF) membrane filter (Millex-HV, Millipore®, USA) to remove microbial and particle interference.

DOM UV-Vis absorbance and fluorescence measurements (excitation-emission matrices, EEMs) were obtained by an Aqualog® absorption-fluorescence spectrometer (Horiba, Japan). Milli-Q® water served as the blank for Raman peaks subtraction. Absorbance was scanned over the range 230 to 800 nm at 1 nm intervals. The Napierian absorption coefficient $a(\lambda)$ was calculated using the equation $a(\lambda) = 2.303 \times A/l$, where A is the absorbance, and l is the cuvette path length (m), following the methods described by Coble (2007) and Helms et al. (2008). The absorption coefficient at 355 nm normalized for DOC concentration, i.e., a_{355}/DOC , has been used as a surrogate for the abundance of chromophoric DOM (CDOM). Specific ultraviolet absorbance at 254 nm (SUVA_{254}), representative of DOM aromaticity, is defined as the ultraviolet absorbance at 254 nm normalized for DOC concentration. The spectral slope ($S_{275-295}$) was calculated from the absorbance spectra by the nonlinear exponential fitting function and served as a proxy for the molecular weight of CDOM.

Fluorescent DOM emission-excitation matrices (EEMs) were recorded from the fluorescence spectra with a 150 W ozone-free xenon lamp and a 10 mm quartz cuvette. Emission spectra were collected from 250 to 620 nm at 3.18 nm increments, and excitation spectra from 230 to 450 nm at 5 nm intervals. The fluorescence index (FI), biological index (BIX) and humification index (HIX) were calculated from the fluorescence spectra. FI thresholds of below 1.4 and above 1.9 were applied to distinguish autochthonous and allochthonous sources of fluorescent DOM (FDOM) respectively. Four fluorescent components were determined based on characteristic EEM peaks, including two humic-like components expressed by peak A ($E_x/E_m = 250\text{--}260\text{ nm}/380\text{--}480\text{ nm}$) and Peak C ($E_x/E_m = 330\text{--}350\text{ nm}/420\text{--}480\text{ nm}$), and two protein-like components represented by peak B ($E_x/E_m = 270\text{--}280\text{ nm}/300\text{--}320\text{ nm}$) and peak T ($E_x/E_m = 270\text{--}280\text{ nm}/320\text{--}350\text{ nm}$) (Coble et al., 2014). EEMs were automatically corrected for the inner-filter effect using the Aqualog® EEMs data processing software, incorporating parallel absorbance measurements from both the same sample and the blank (Yang and Hur, 2014).

2.3 FT-ICR MS Measurements

A subset of 26 samples, including 17 lake samples (14 Cuona Lake, 2 CJ and 1 GN), 9 river samples including BSQ, SQ, ZGQG, WGQ and 1 NQ river, were analyzed for molecular composition via FT-ICR MS. The filtered (0.22 μm), acidified (pH 2 using 10 mol L⁻¹ HCl) samples were solid-phase extracted (SPE) by 6 mL PPL cartridges (Agilent) and eluted using methanol and subsequently dried by N₂ purging (Dittmar et al., 2008; Spencer et al., 2015). The enriched filtrates were performed molecular characterization using a Bruker Solarix FT-ICR MS equipped with a 15.0 T superconducting magnet and an ESI ion source in negative mode. Peaks of a signal-to-noise ratio (S/N) ≥ 3 were assigned to potential formulas including combinations of C_{40–50}H_{2–87}O_{1–52}N_{0–5}S_{0–3}P_{0–2} atoms. The assigned formulas can be classified into several compound groups according to the modified aromaticity index (AI_{mod}) (He et al., 2016), H/C and O/C values (Hertkorn et al., 2006): lipids (O/C = 0–0.2, H/C = 1.7–2.2), proteins (O/C = 0.3–0.67, H/C = 1.5–2.2), lignin (O/C = 0.1–0.6, H/C = 0.6–1.7), tannins (O/C = 0.6–1.2, H/C = 0.5–1.5), unsaturated hydrocarbons (O/C = 0–0.1, H/C = 0.7–1.5), and condensed aromatic structures (H/C = 0.2–0.7, O/C = 0–0.67). Carboxylic-rich alicyclic molecules (CRAM) are defined based on Hertkorn et al. (2006). AI_{mod} was calculated according to Eq. (1).

$$AI_{mod} = \left[1 + C - \frac{1}{2} \times O - \frac{1}{2}(N + H) \right] / \left(C - \frac{1}{2} \times O - N \right)$$

1

2.4 HPLC-SEC Analysis

High-performance liquid chromatography-size exclusion chromatography (HPLC-SEC) was conducted to measure molecular weight (MW) distribution of dissolved organic matter. Briefly, 20 μL of sample aliquots were separated on an exclusion column (LC-20AD). The mobile phase consisted of phosphate-buffered saline (PBS; 137 mM NaCl, 2.7 mM KCl, 4.3 mM Na₂HPO₄, 1.4 mM KH₂PO₄, pH 7.2–7.4), delivered at a flow of 0.8 mL min⁻¹. Detected was performed with a UV-Vis detector (SPD-20A) at 254

nm. Chromatograms were acquired and processed using peak integration and molecular weight calculation software. Polystyrenesulfonate (PSS) standards with nominal molecular weights of 370, 580, 945, 1230, 1920, 3090, 4750, 6320, and 9570 Da were used for the calibration. Based on the chromatographic profile, DOM was sliced into three molecular weight fractions: low-molecular-weight (LMW, MW < 5000 Da), medium-molecular-weight (MMW, MW ranged 5000–9570 Da), and high-molecular-weight (HMW, MW > 9570 Da) components. The number-averaged molecular weight (M_n) and weight -averaged molecular weight (M_w) were calculated according to the following equations (Striegel et al., 2009):

$$M_n = \frac{\sum_{i=1}^N h_i}{\sum_{i=1}^N (h_i / M_i)}$$

2

and

$$M_w = \frac{\sum_{i=1}^N (h_i M_i)}{\sum_{i=1}^N h_i}$$

3

Where h_i is the SEC curve height at the i th volume increment and M_i is the molar mass of the species eluted at the i th retention volume which is calculated by the calibration curve. The equation assumes that h_i is proportional to solute concentration and M_i is sampled in equal volume increments.

2.5 Water Stable Isotopes and Water Chemistry

All water chemistry parameters, except for those measured in situ, were analyzed in the laboratory. Chloride (Cl^-) concentration was determined by ion chromatography, and bicarbonate (HCO_3^-) concentration was measured by acid titration. Stable hydrogen and oxygen isotope ratios in natural waters serve as effective tracers for identifying water sources and provide insights into hydrological conditions such as connectivity and evaporative loss. Water stable isotopes in all collected samples ($n = 20$) were measured using an LGR L2130-i laser absorption spectrometer (model: 190327; Los Gatos Research, Inc., CA, USA), which provides information of sufficient precision comparable to that of an isotope ratio mass spectrometer. $\delta\text{D-H}_2\text{O}$ and $\delta^{18}\text{O-H}_2\text{O}$ were calculated as following equation:

$$\delta \text{ (‰)} = [(R_{\text{measured}} - R_{V-SMOW}) / R_{V-SMOW}] \times 1000$$

4

where R is atomic ratio, $\text{D}/^1\text{H}$ or $^{18}\text{O}/^{16}\text{O}$; $V - SMOW$ showing the Vienna Standard Mean Ocean Water. The precision of $\delta\text{D-H}_2\text{O}$ and $\delta^{18}\text{O-H}_2\text{O}$ was $\leq 1.3\text{‰}$ and $\leq 0.5\text{‰}$, respectively.

2.6 Statistical Analysis

Statistical analyses, including Spearman correlation, linear regression analyses, dataset normality test, and calculations of mean values with standard deviation (Mean $\pm$ SD), were performed using Origin Pro® 2021. All calculations for FT-ICR MS dataset were conducted in MATLAB R2024a. All figures were generated using the 'ggplot2' package (Wickham, 2016) in R version 4.4.2 (R Core Team, 2022). Kriging interpolation analysis was carried out with ArcMap10.8. Results of Spearman rank correlations (r_s) with $p < 0.05$ levels was considered statistically significant.

3 Results

3.1 Water Stable Isotopes and Water Chemistry Variability

During the wet season, pH values across the Cuona continuum ranged from 7.9 to 9.0, with an average of 8.11 ± 0.16 (Table S1). Dissolved oxygen (DO) concentration varied between 4.1 and 9 mg L⁻¹, averaging 5.12 mg L⁻¹, and generally increased toward Cuona Lake (CN) in the outflow direction. Total dissolved solids (TDS) concentrations ranged from 228 to 635 mg L⁻¹, which were lower than those reported for other saline lakes on the plateau (Wang et al., 2009). The concentration of chloride ion varied from 2.8 to 156 mg L⁻¹, with an average value of 17.08 ± 3.02 mg L⁻¹. The average bicarbonate (HCO₃⁻) concentration was 218.6 ± 52.81 mg L⁻¹, with the highest value observed in ZGQG and the lowest in GN Lake (Table S1).

Stable isotopes of hydrogen and oxygen in lake water were used to evaluate the extent of hydrological connectivity and evaporation in the Cuona continuum (Fig. 2). $\delta^{18}\text{O}_{\text{V-SMOW}}$ gets enriched faster than $\delta\text{D}_{\text{V-SMOW}}$ during evaporation, contributing to a lower slope of the local evaporation line (LEL) than the global meteoric water line (GMWL) (Brooks et al., 2014). As expected, the LEL in the studied area exhibited a clockwise shift away from the GMWL. Only a few river samples approximately near the GMWL (Fig. 2), indicating contributions from surrounding inflow rivers. The intersection of the LEL and the GMWL provides an estimate of the source of lake water (input water), occurred at a $\delta^{18}\text{O}_{\text{V-SMOW}}$ value of -17.45‰. This low LEL intersection is consistent with findings from polar lakes and supports a dominant contribution from glacial meltwater and snowmelt. The water isotopes in inflow lake (CJ Lake: $\delta^{18}\text{O}_{\text{V-SMOW}}$: -5.19‰; $\delta\text{D}_{\text{V-SMOW}}$: -54.7‰) were overall enriched than those in river samples ($\delta^{18}\text{O}_{\text{V-SMOW}}$: -17.77‰ ~ -14.63‰; $\delta\text{D}_{\text{V-SMOW}}$: -136.7‰ ~ -108.1‰) and samples from Cuona Lake ($\delta^{18}\text{O}_{\text{V-SMOW}}$: -15.34‰ ~ -7.87‰; $\delta\text{D}_{\text{V-SMOW}}$: -114.6‰ ~ -71.7‰). The value of water isotopes increased substantially from upstream to downstream lakes (Fig. 2), reflecting cumulative evaporation effects. Water inputs, precipitation, and evaporation collectively exerted a decisive impact on water storage change in Cuona Lake. A positive relationship was observed between water isotopes and chloride concentration, supporting an ideal proxy for $\delta^{18}\text{O}$ or δD to explore the influence of hydrological conditions on DOM characteristics across the aquatic continuum (Fig. 2b).

3.2 DOM Concentrations and Optical Characteristics

During the sampling period, the average dissolved organic carbon (DOC) concentration in Cuona Lake (CN lake; average DOC: $4.69 \pm 0.55 \text{ mg L}^{-1}$) was overall lower than those of inflow rivers (average DOC $7.13 \pm 3.49 \text{ mg L}^{-1}$) and lake (CJ lake; average DOC: $12.04 \pm 1.01 \text{ mg L}^{-1}$) (Fig. S1a). The highest DOC concentrations were observed in CJ Lake and the BSQ, while the lowest occurred in the central region of Cuona Lake (CN/M). Chromophoric dissolved organic matter (CDOM) levels, particularly in BSQ and ZGQG, were significantly higher than those in Cuona Lake and its connected lakes (Fig. S1b). The specific ultraviolet absorbance at 254 nm (SUVA_{254}), an indicator of DOM aromaticity, decreased gradually along the flow path (Fig. S1c). The average SUVA_{254} values in Cuona Lake was lower than that in recharging rivers and lakes. However, The SUVA_{254} values in the northern part of Cuona Lake (CN/N) were slightly higher than in other sections, likely due to the substantial inflow from ZGQG and SQ and strong in-lake mixing. As the primary zone receiving terrestrial organic matter from river inputs, CN/N exhibited correspondingly higher DOC concentrations and DOM aromaticity. Accordingly, the value of $S_{275-295}$, which is inversely proportional to DOM molecular weight, ranged from 0.013 to 0.047 nm^{-1} across all samples (Fig. S1d). The $S_{275-295}$ values indicated that DOM molecular weight was significantly larger in rivers than in other waters of the Cuona continuum.

The fluorescence index (FI) was considered a proxy for DOM sources. FI values across the Cuona continuum ranged from 1.18 to 2.3, reflecting mixed contributions from both terrestrial inputs and autochthonous production (Fig. S2c). Riverine DOM generally exhibited FI values near 1.4, suggesting a dominant terrestrial origin derived from surface runoff, soil leaching, flood inputs, and the release of aged organic matter from glacial and permafrost melt. In contrast, lake DOM showed FI values closer to 1.9, indicating a stronger autochthonous signal. The long hydrological retention time in Cuona Lake facilitates microbial activity and phytoplankton growth, resulting in DOM shows a strong autochthonous signature. As for the EEM-derived fluorophores, four fluorescence characteristic peaks were identified in all samples. The mean fluorescence intensity of humic-like components (Peak C) was higher in rivers than in Cuona Lake (Fig. S2a). Among the lakes, Cuoja Lake (CJ) contained the most abundant protein-like components (Peak B). In comparison to other water samples, Cuona Lake displayed the lowest fluorescence intensities for both humic-like and protein-like components.

3.3 DOM Molecular Weight in the Aquatic Continuum of Cuona Lake

High-performance size exclusion chromatography (HPSEC) was performed to analyze DOM molecular weight distributions, providing complementary validation of optical-based observations regarding compositional shifts between lake and riverine DOM. The weight-averaged molecular weight (M_w) and number-averaged molecular weight (M_n) of all DOM samples ranged from 3083 to 4383 Da and 2414 to 4102 Da, respectively (Table S2). DOM in the Cuona continuum was predominantly composed of low molecular weight (LMW (%); $<5000 \text{ Da}$) and medium molecular weight (MMW (%); $5000 \sim 9570 \text{ Da}$)

fractions (Fig. 3a). Cuona Lake exhibited the highest mean relative abundance of LMW DOM compared to rivers, whereas the largest proportion of MMW DOM was observed in BSQ.

3.4 DOM Molecular Composition Identified by FT-ICR MS

DOM molecular composition was further analyzed using FT-ICR MS to obtain molecular-level fingerprints and assess DOM chemical diversity. Across all samples, a total of 5377 ~ 7593 unique formulas were identified with an average of 6532 ± 524 formulas in each sample (Fig. S3a). The number of assigned formulae was overall lower in Cuona Lake than that of connected rivers and lakes. For Cuona Lake, the northern and eastern samples (CN/N and CN/E) exhibited the lowest values (Fig. S3). The distribution of DOM molecular formulae numbers throughout the Cuona continuum indicate the primary contribution of inflowing water to DOM molecular diversity in Cuona Lake. The majority of the molecular formulas were CHO-containing (30.97 ~ 46.69%, mean = $40.82\% \pm 3.49\%$), followed by nitrogen-containing (CHON, 28.98 ~ 37.18%, mean = $33.89\% \pm 2.26\%$), sulfur-containing (CHOS, 6.84 ~ 20.3%, mean = $11.39\% \pm 2.99\%$), and phosphorus-containing (CHOP, 2.43 ~ 7.23%, mean = $5.19\% \pm 1.28\%$), and nitrogen- and sulfur-containing (CHONS, 1.94 ~ 8.98%, mean = $3.97\% \pm 1.53\%$) molecular formulae in all samples (Fig. S4). Aquatic DOM in the Cuona Lake continuum consists mainly of CHO- and CHON- compounds, which exhibit high hydrophilicity and are enriched with acidic functional groups of hydroxyl (OH^-) and carboxyl (COOH^-) that can bind heavy metal ions (Dong et al., 2011; Wang et al., 2021). Most CHO- and CHON-containing formulas were defined as highly unsaturated and aromatic compounds, whereas unsaturated compounds were predominantly composed of CHOP-containing molecules (Fig. S7). The modified aromaticity index (Al_{mod}) was lowest in Cuona Lake and highest in the BSQ river (Fig. S5). The values of Al_{mod} , which directly reflect DOM aromaticity at molecular level, were in accordance with optical values of SUVA_{254} . Nominal oxidation state of carbon (NOSC), indicative of the redox state of molecular DOM, reflecting the biogeochemical activities and bioavailability of DOM molecules (LaRowe et al., 2011). Across all samples, riverine DOM was more oxidized, while lake DOM was more reduced, indicating higher biogeochemical reactivity in river DOM than in lake DOM (Fig. S6). A portion of the molecular formulas were classified as highly unsaturated and carboxyl-rich alicyclic molecules (CRAM). These are characterized by abundant CHO, CHNO and a small amount of CHOS, and a core alicyclic structure with carboxyl-rich branched chains (Cai et al., 2023).

The majority of assigned molecular formulae were classified as lignins (58.94 ~ 71.73%, mean = $66.34\% \pm 3.46\%$) and tannins (8.37 ~ 13.85%, mean = $11.1\% \pm 1.14\%$), with higher average proportions observed in riverine dissolved organic matter (DOM) compared to Cuona Lake samples (Fig. 4a). Across Cuona Lake, the CN/N region exhibited greater abundances of lignin and tannin compounds than other areas, which could be attributed to the input of ZGQG and SQ. (Fig. S3b). These relative abundances align with spectral aromaticity parameters, indicating that aromatic DOM primarily originates from terrestrial plant-derived materials riched in lignin and tannin. The predominance of lignin- and tannin-like molecules in riverine DOM further supports a substantial terrestrial contribution (Fig. S3b). Lignin content in Cuojia Lake was slightly lower than in Cuona Lake, suggesting that terrestrial DOM in Cuona Lake is not directly

supplied by Cuojia Lake. Instead, terrestrial DOM in Cuona Lake appears to be mainly replenished by surrounding rivers rather than upstream lakes. Lignin-like compounds are associated with DOM molecular activity (Wen et al., 2025), and their high abundance in rivers indicates high biogeochemical activity, which is consistent with NOSC values (Fig. S6). In contrast, molecular formulae representative of lipid (5.45 ~ 17.35%, mean = $10.83\% \pm 3.25\%$), protein (1.42 ~ 5.69%, mean = $3.59\% \pm 1.26\%$) and amino sugar (1.26 ~ 2.5%, mean = $1.8\% \pm 0.36\%$) showed higher mean relative abundances in Cuona and Cuojia Lakes than in rivers, with a decreasing trend observed along the flow path in the effluent GN Lake (Fig. S3b). Molecular formulae categorized as lipid, protein and amino sugar are typically associated with fresh, recently produced or biolabile DOM, implying stronger microbial and phytoplankton activity in lakes relative to rivers. For DOM molecular composition, no significant replenishment relationship or shared origins was observed between Cuojia and Cuona Lakes.

4 Discussion

4.1 DOM Turnover and Distribution Along the Aquatic Continuum of Cuona Lake

The DOC concentrations across the Cuona continuum were generally lower than those in Ontario, Canada (Hill et al., 2009), but slightly higher than those in major inland rivers such as the Pearl River Estuary, the Yellow River and the Yangtze River (Covert et al., 2001; Zhang et al., 2013; Wang et al., 2019). Alpine rivers in the region exhibited lower DOC concentrations compared to other large North American rivers (Cai et al., 2015; Mann et al., 2016). Similar to reports in other semiarid regions (Kellerman et al., 2019; Zhou et al., 2017), Cuona Lake showed lower DOC levels relative to saline lakes, which could be attributed to shorter water retention time and more intense hydrodynamic conditions. For all samples, DOC concentration was significantly and positively correlated with CDOM (Fig. 3b). This finding is consistent with observations in most freshwater lakes and marine systems (Zhang et al., 2005; Matsuoka et al., 2013), while contrasting with findings from certain saline lakes on the QTP, such as Rencuo Lake (Wang et al., 2025). The results indicated that DOC in alpine rivers and lakes is predominantly composed of chromophoric DOM, supporting the use of spectral measurements for monitoring and predicting DOC concentrations in remote QTP freshwater systems.

Within the Cuona continuum, DOC concentration was relatively higher in CJ Lake compared to Cuona and GN Lakes (Fig. S8a), showing a decreasing trend along flow path with the contribution of DOM mineralization and photodegradation. In Cuona Lake, DOC concentrations decreased from the shore toward the center, possibly as a result of strong hydrodynamic mixing (Fig. S8a). Medium molecular weight DOM (MMW), which is relatively refractory and photolabile, was more abundant in CN/N. (Fig. S8b; S8d), reflecting substantial inputs of terrestrial humic-like materials derived from glaciers, permafrost, and soils (Stubbins et al., 2010). This interpretation is further supported by the spatial distribution of chromophoric DOM within Cuona Lake (Fig. S8c).

To elucidate variations in dissolved organic matter along the aquatic continuum of Cuona Lake, molecular turnover in response to the river–lake transport pathway was identified. During inflow from Cuojia (CJ) to Cuona (CN) Lake, 10% of assigned molecular formulae were degraded, including 21% of protein- and lipid-like compounds, while 5% of lignin-like and 23% of tannin-like molecules were produced (Fig. 5). Along the pathway from rivers to CN Lake, 5% of total molecular formulae and 8% of lignin and tannin molecules were degraded, whereas protein and lipid molecules increased by approximately 95% and 80%, respectively. In the outflow from CN to Ganong Ma (GN) Lake, changes in formula abundances and lignin molecules were less pronounced than during inflow, except for recently produced protein-like molecules and a marked 30% decrease in NOSC values. In this process, 14% of protein compounds were degraded (Fig. 5). These results indicate that rapid turnovers of DOM molecular compositions in the Cuona continuum, especially in river-lake continua with strong hydrological connectivity. During inflow, a substantial fraction of terrestrial DOM was degraded into protein and lipid molecules through photochemical and biological activities (Fig. S9a). The higher abundance of CHOP-containing compounds in Cuona Lake compared to rivers further supports the in-situ production of hydrophilic protein- and lipid-like molecules in downstream lakes (Fig. S4). In contrast, DOM turnover between lakes (e.g., from CJ to CN) was less pronounced than in river-lake transitions, likely due to weaker hydraulic gradients in lacustrine systems. During outflow, key changes included the degradation of protein- and lipid-like molecules and the production of lignin- and tannin-like compounds, leading to an enrichment of condensed aromatic and lignin-like molecules in GN Lake (Fig. S9c). Additionally, DOM biogeochemical activity and bioavailability decreased along the outflow path, as reflected by lower NOSC values (Fig. S6).

4.2 Variation of DOM Composition and Molecular Weight Along the Fluvial Pathway

Both the value of CDOM and $SUVA_{254}$ significantly decreased from upstream to downstream along the fluvial pathways (Fig. 6b; 6c), likely resulting from a combination of biodegradation (Li et al., 2019; Spencer et al., 2014), quick photo-oxidation (Jennings et al., 2020) or dilution (Du et al., 2021). A similar declining trend has been reported for the St. Louis River in Minnesota and Wisconsin, U.S.A (Berg et al., 2019). Besides microbial degradation, photobleaching of chromophoric DOM is an important process during hydrological transport, especially in high-altitude lakes with intense solar irradiance (Cory et al., 2013; 2014). Consequently, the decline in the value of $SUVA_{254}$ reflects a marked loss of aromatic compounds along the river continuum. Moreover, a gradual decrease in DOM molecular weight was also observed (Fig. 6d), indicating rapid degradation and mineralization of terrestrial organic matter along the flow path. The decrease in $S_{275-295}$ agrees with the direct observation of reduced medium-molecular-weight (MMW) DOM and increased low-molecular-weight (LMW) DOM (Fig. 6e; 6f). Such photodegradation-induced shifts from high- to low-molecular-weight organic matter have been widely documented (Helms et al., 2018; Stubbins et al., 2010). Furthermore, MMW can be transformed into LMW through photodegradation, contributing to higher MMW and lower LMW fractions in rivers compared to Cuona Lake. This process partly explains the notable reduction in formula numbers from rivers to the lake (Fig. S3). Changes in the relative intensity of humic-like components (reflected by

CDOM and SUVA₂₅₄) followed trends similar to DOC concentration but opposite to $S_{275-295}$ values (Fig. 6). The lowest relative abundances of LMW DOM and molecular formula numbers in Cuona Lake provide further evidence for the loss of aromatic compounds (Fig. 3a).

From the upper to lower reaches of the BSQ and ZGQG rivers, CDOM and SUVA₂₅₄ decreased, while $S_{275-295}$ increased. In contrast, the SQ river exhibited a downstream increase in both CDOM and SUVA₂₅₄ (Fig. 6b; 6c), likely due to extensive marsh growth and pastoral activities near the shore, which enhanced the input of aromatic and chromophoric DOM. The observed downstream decrease in DOM aromaticity, chromophore abundance, and molecular weight in the pristine BSQ and ZGQG rivers, as opposed to the increase in anthropogenically influenced SQ river, demonstrates that ambient conditions and human activities are key factors controlling DOM characteristics. In rivers undisturbed by human or pastoral activities, DOM properties appear to be governed primarily by natural biogeochemical processes such as photodegradation and mineral adsorption, leading to reduced aromaticity, photoreactivity, and molecular weight along the flow path. These results contrast with findings from anthropogenically disturbed, non-pristine rivers in the Lake Nam Co watershed (Maurischat et al., 2022), underscoring the pronounced impact of human land use on DOM composition. Results indicated DOM composition shifts from terrestrially derived DOM towards more processed, microbial/algal-derived DOM as water moves from upper rivers to downstream reaches. This transition is also evidenced by the decreases in molecular weight and aromaticity, along with the increases in saturation and DOM chemodiversity.

4.3 Response of DOM Molecular Weight and Composition on Hydrological Conditions

In the study, δD_{V-SMOW} was served as an indicator to explore the linkages between hydrological conditions and DOM composition. Significant positive relationships were observed between water isotope values and both $S_{275-295}$ and BIX, whereas negative relationships were found with CDOM and SUVA₂₅₄ (Fig. 7). The fluorescence intensities of humic-like components—including the lower molecular weight peak A and the more refractory, high molecular weight peak C, both indicative of terrestrial DOM inputs—also showed significant negative correlations with water isotope values (Fig. 7). Additionally, water isotopes were positively correlated with low-molecular-weight (LMW) DOM and negatively correlated with medium-molecular-weight (MMW) DOM (Fig. 7). Enriched water isotopes in lakes, associated with prolonged ultraviolet exposure and longer water retention time, facilitate DOM photodegradation (Du et al., 2020). This process contributes to marked decreases in DOM aromaticity, molecular weight, and the abundance of photosensitive humic-like components from upstream to downstream, and may further explain the the lowest number of molecular formulae and AI_{mod} observed in Cuona Lake. Longer water retention allows more time for DOM geochemical processing, as previously reported in Swedish boreal lakes (Kellerman et al., 2014; Kothawala et al., 2014). Furthermore, unique molecular components in lakes were primarily comprised of protein- and lignin-like compounds, whereas those in rivers were dominated by terrestrial tannins and condensed aromatics (Fig. 4b). This

compositional distinction supports the negative correlations between water isotope values and humic-like components represented by SUVA₂₅₄, Peak A and Peak C (Fig. 7).

Accordingly, DOM molecular formulae significantly correlated with water isotopes were categorized as protein-like, lignin-like, tannin-like, and highly unsaturated compounds (Fig. 8). Specifically, water isotopes correlated positively with protein and lipid formulas but negatively with lignin, tannin, and condensed aromatic formulas in the van Krevelen diagram (Fig. 8a), suggesting that samples with relatively enriched δD_{V-SMOW} were associated with a higher abundance of proteinaceous or aliphatic materials. These molecules typically exhibit lower aromaticity and molecular weight. The observed relationships between water isotope values and DOM molecular weight/composition provide strong evidence for hydrological regulation of DOM biogeochemical reactivity along the Cuona Lake continuum.

Water isotopes reflect evaporation intensity and hydrological connectivity in aquatic systems and are highly associated with water sources. Enriched water isotopes were associated with depleted DOM aromaticity and molecular weight, as well as enhanced microbial and phytoplankton activity—supported by correlations with humic-like components (Peak A and Peak C), SUVA₂₅₄ and $S_{275\sim 295}$ (Fig. 8). These patterns can be attributed to extended light exposure and longer water retention time in downstream lacustrine environments. Furthermore, the relationship between water isotopes and molecular formulas was stronger in lakes than in rivers (Fig. 8a; 8c), indicating that hydrological processes exert a more dominant control on DOM composition in lacustrine systems. In contrast, riverine DOM is more influenced by local ambient conditions—such as catchment vegetation, hydraulic erosion, and pastoral activities—reflecting shorter water residence times and more direct human-induced disturbances. Similar relationships between water isotopes and DOM characteristics have been reported in other sparsely populated watersheds, including the Yukon River Basin (Johnston et al., 2020), Selin Co watershed (Zhou et al., 2023), coastal southeast Alaska (Fellman et al., 2014; Holt et al., 2021), and deglaciated catchments in western Greenland (Kellerman et al., 2019). It is noteworthy that hydrological conditions play a dominant role in regulating DOM molecular weight and composition in lakes governed by natural processes. This contrasts with findings from anthropogenically impacted rivers or lakes, where factors such as pastoral activities, land use, and population density become the primary drivers of DOM biogeochemistry (Zhou et al., 2021, 2022).

5 Conclusion

Riverine transport of terrestrial and glacial dissolved organic matter (DOM) into alpine lakes is a crucial process in the global carbon cycle. In this study, we observed rapid turnover of dissolved organic carbon (DOC) concentration and DOM compositions along the Cuona continuum, especially in river-lake continua characterized by strong hydrological connectivity. During inflow, a substantial fraction of terrestrial DOM was degraded into protein and lipid molecules through potential environmental processes. Terrestrial DOM in Cuona Lake was found to be primarily supplied by rivers rather than upstream lakes. DOM across the Cuona continuum was predominantly composed of low-molecular-weight (LMW (%); <5000 Da) compounds. In contrast to saline lakes, DOM in alpine freshwater lakes and

rivers was mainly composed of chromophoric DOM, supporting the use of optical measurements for monitoring and predicting DOC concentrations in remote freshwater lakes of the Qinghai-Tibet Plateau.

Both optical and molecular-level analyses confirmed systematic variations in DOM composition and molecular weight along the Cuona continuum. Overall, DOM becomes less aromatic, less colored, and lower in molecular weight along the fluvial pathway. These compositional changes may allow DOM more photolabile, and bioavailable to microbial utilization, potentially altering microbial metabolic pathways. Results indicated DOM composition shifts from terrestrially derived DOM towards more processed, microbial/algal-derived DOM as water moves from upper rivers to downstream reaches. Molecular-level changes aligned with optical signatures, including decreases in SUVA_{254} and CDOM, and increases in $S_{275-295}$. The consistency of results regarding variations in DOM composition—demonstrated by optical analysis, high-resolution molecular characterization, and molecular weight measurements—indicates that simple optical parameters can effectively capture bulk DOM compositional changes in these remote aquatic systems.

Furthermore, we traced shifts in DOM molecular composition in response to hydrological connectivity, revealing molecular-level mechanisms driving DOM transformation. Changes in DOM composition exhibit a stronger response to hydrological conditions in lakes predominantly governed by natural processes than in rivers primarily influenced by anthropogenic factors. Our results underscore the significance of hydrological conditions in modulating DOM dynamics, which is essential for predicting DOM changes and biogeochemistry in aquatic carbon cycling. These findings further emphasize the role of water retention time (WRT) as a key predictor of changes in DOM quantity and quality. Under ongoing climate warming, the hydrological regime of the QTP is undergoing rapid changes. Rising temperatures, characterized by glacier melt and altered precipitation-evaporation patterns, have led to significant expansion of lake area and volume, as well as lengthened water residence times across the region. These changes allow extended time for DOM processing—including photodegradation, microbial utilization, and autochthonous production—within alpine aquatic systems. The observed depletion of DOM along fluvial pathways may be partly attributed to its mineralization into carbon dioxide, contributing to greenhouse gas emissions from lakes and thereby exacerbating global warming. Collectively, these findings indicate that alpine lakes on the Tibetan Plateau are poised to play an increasingly active and prominent role in regional and global carbon cycles under future climate scenarios.

Abbreviations

DOM Dissolved organic matter; **QTP** Qinghai-Tibet Plateau; **CDOM** Chromophoric dissolved organic matter; **UV-Vis** Ultraviolet-Visible; **EEM** Excitation-emission matrix; **FT-ICR-MS** Fourier transform ion cyclotron resonance mass spectrometry; **HPLC-SEC** High-performance liquid chromatography-size exclusion chromatography; **BIX** Biological index; **FI** Fluorescence index; **HIX** Humification index; **FDOM** Fluorescent DOM; **LEL** the local evaporation line; **GMWL** the global meteoric water line; **LMW** low-

molecular-weight; **MMW** medium-molecular-weight; M_n The number-averaged molecular weight; M_w weight -averaged molecular weight.

Declarations

Author contributions

All authors contributed to the study conception and design. Material preparation, data collection and analysis were performed by Yuqin Wang, Junchuan Huang, Min Zhang, Pei Liu, Jianxun Cui, Xiaomei Cui, Wangchuan Guo, Jungui Zhang, Congxin Yang. The first draft of the manuscript was written by Yuqin Wang and all authors commented on previous versions of the manuscript. All authors read and approved the final manuscript.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

All data supporting the findings of this study are available within the paper and its Supplementary Information.

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Figures

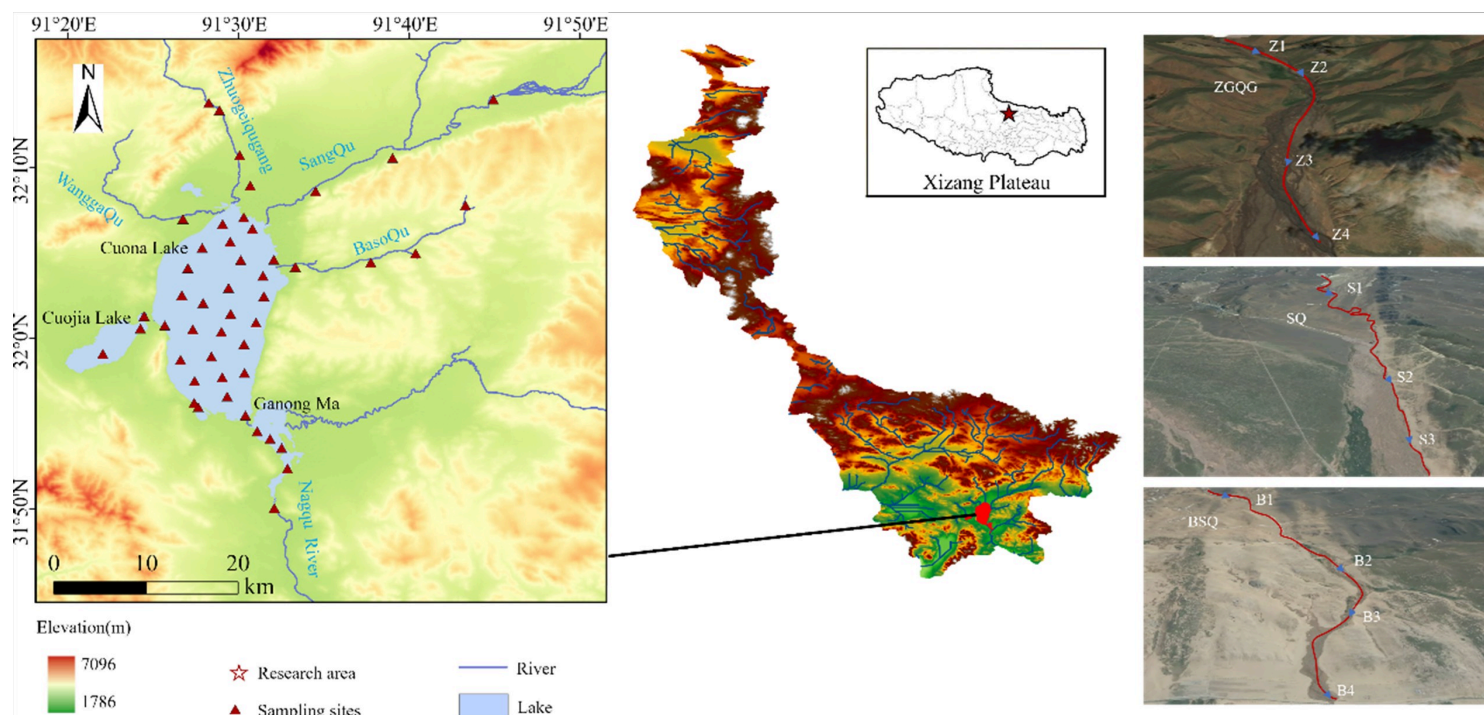


Figure 1

Position of sampling sites in the aquatic continuum of Cuona Lake is located in Anduo County, Xizang Autonomous Region

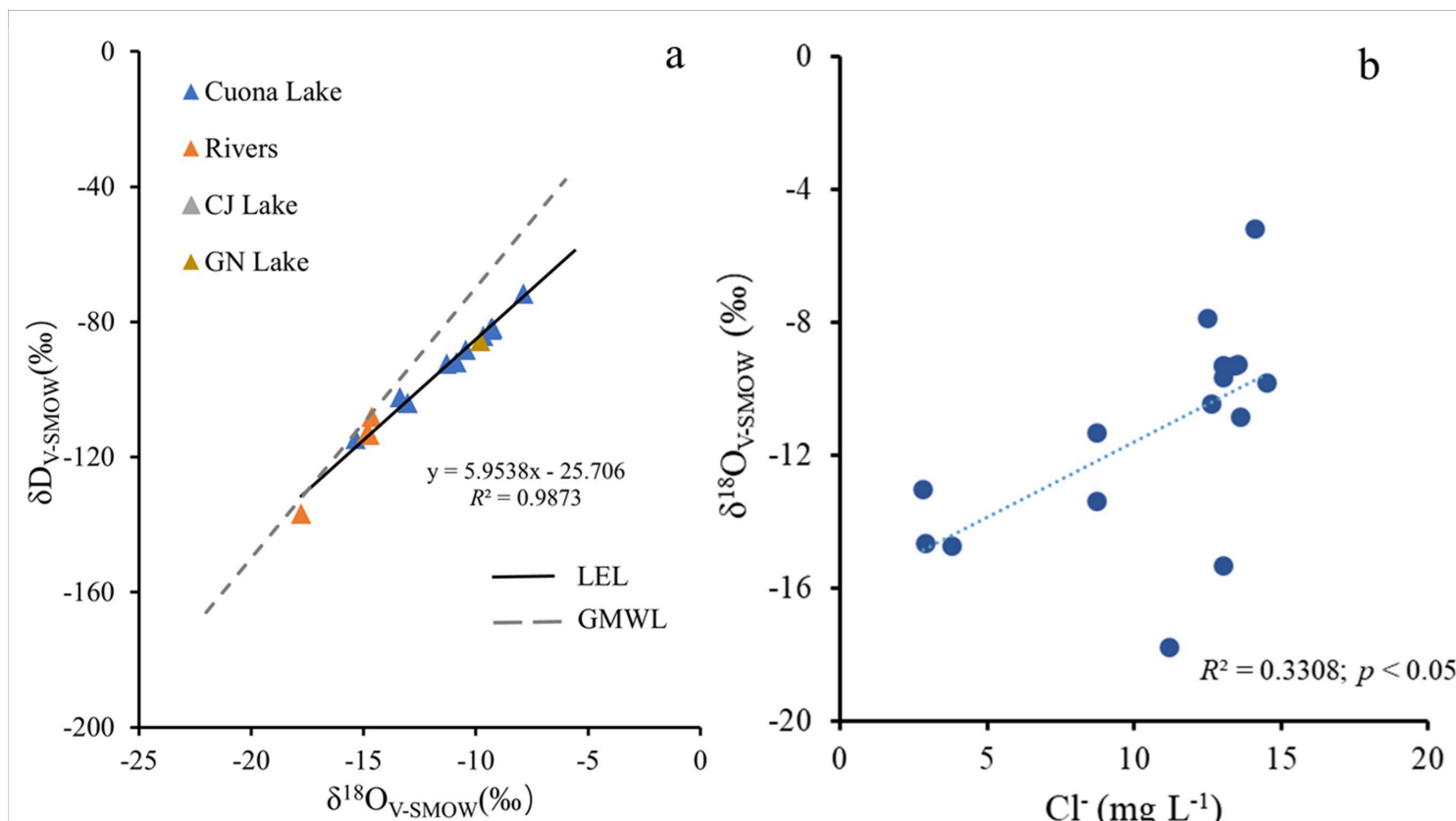


Figure 2

a Characteristics of stable water isotopes in the Cuona continuum. Water isotopes subset including the Cuona Lake, the recharge rivers of BSQ, SQ, WGQ and ZGQG, Cuojia Lake (CJ Lake) and Ganongma (GN Lake). The dashed line indicates the global meteoric water line (GMWL). Equation of the local evaporation line (LEL, solid line) was calculated from all the collected samples in the aquatic continuum of Cuona Lake. **b** Correlation between water isotope of $\delta^{18}\text{O}_{\text{V-SMOW}}$ and chloride concentration

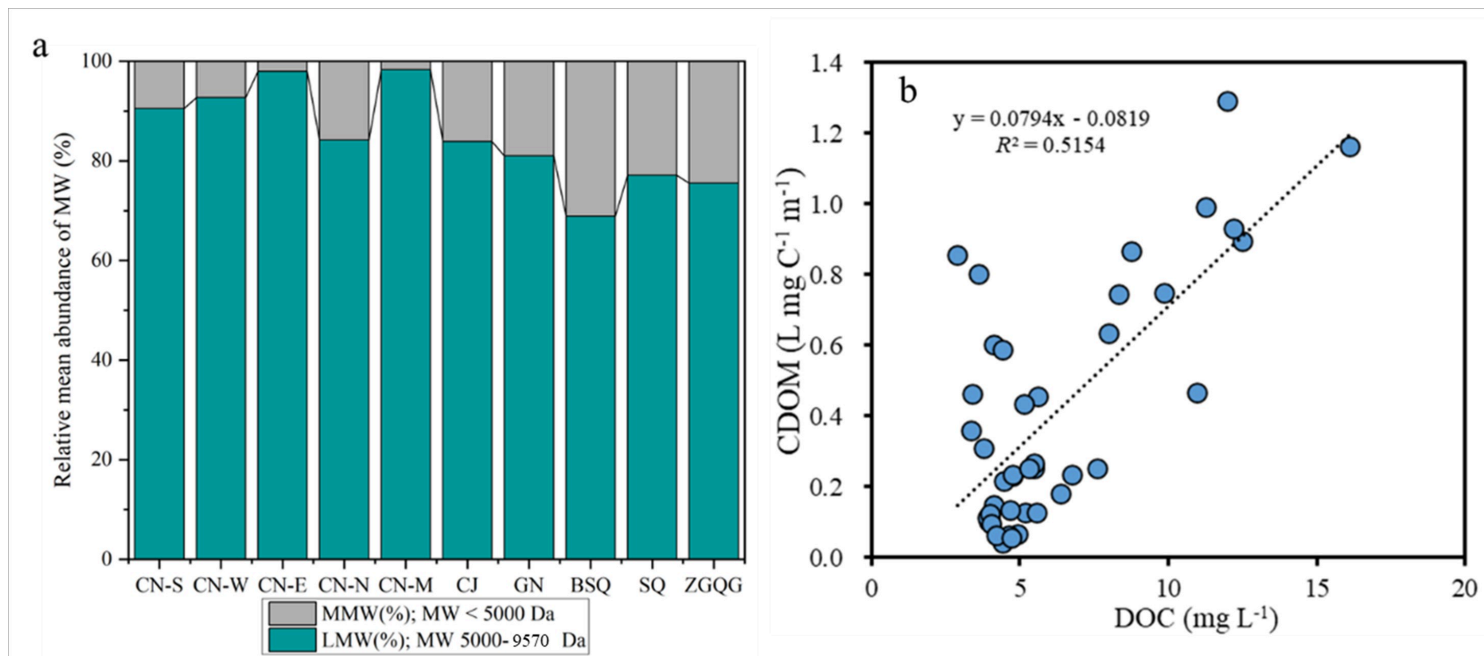


Figure 3

a The relative mean abundances of DOM molecular weight represented by medium-molecular-weight (MMW (%); MW 5000-9570 Da) and low-molecular-weight (LMW (%); MW < 5000 Da). **b** Relationship between the abundance of chromophoric dissolved organic matter (CDOM) and DOC concentration observed of all collected samples in the aquatic continuum of Cuona Lake. The black dashed line indicates the regression line

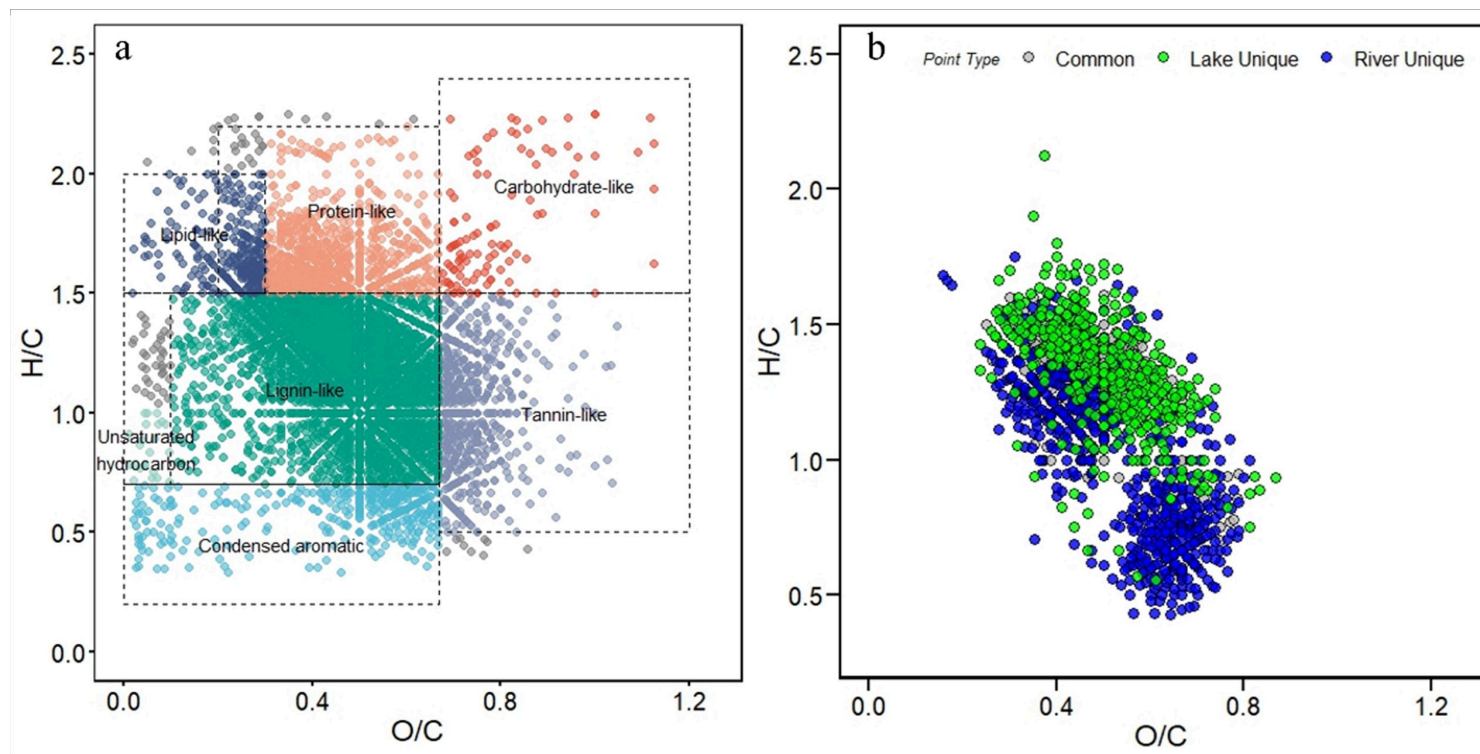


Figure 4

Van Krevelen diagram of all DOM samples collected in Cuona continuum ($n = 26$). **a** The different areas are divided according to the H/C and O/C values, which are marked based on the following criteria: lipids (O/C = 0-0.2, H/C = 1.7-2.2), proteins (O/C = 0.3-0.67, H/C = 1.5-2.2), lignin (O/C = 0.1-0.6, H/C = 0.6-1.7), tannins (O/C = 0.6-1.2, H/C = 0.5-1.5), carbohydrates (O/C = 0.6-1.2, H/C = 1.5-2.2), unsaturated hydrocarbons (O/C = 0-0.1, H/C = 0.7-1.5), and condensed aromatic structures (H/C = 0.2-0.7, O/C = 0-0.67). **b** The unique molecular formulas observed in river and lake DOM. The green dots indicates the unique assigned molecules of lake DOM, the blue dots represent the unique to river DOM, and the grey dots indicates the common molecular formulas both in rivers and lakes DOM

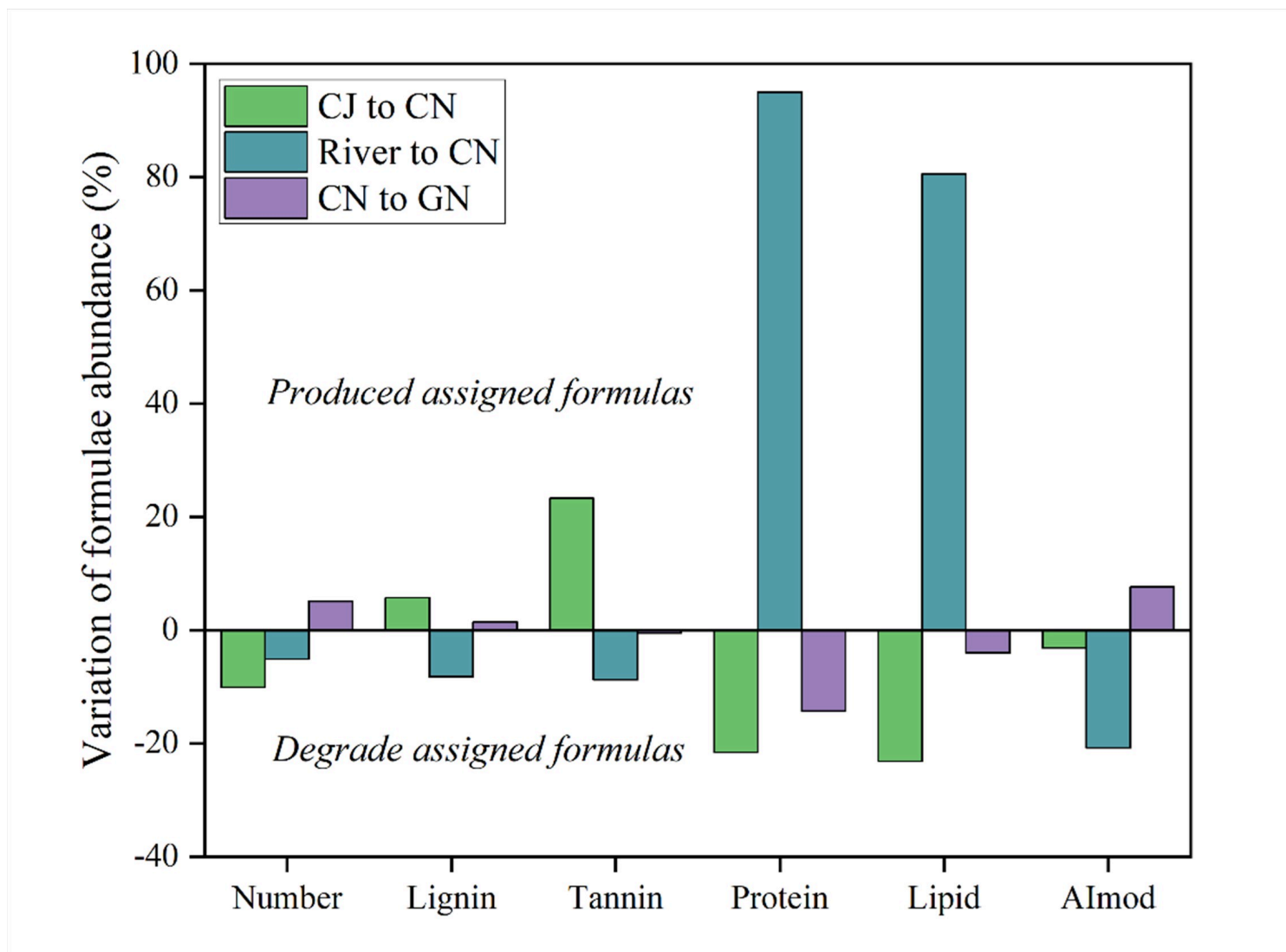


Figure 5

The graphs show DOM molecular turnover response to the continuum pathway of Cuona Lake, including the inflowing variation of Cuojia (CJ) and rivers into Cuona Lake (CN), outflowing variation of Cuona Lake into Ganong Ma (GN). A positive values represents the proportion of newly produced DOM, while a negative value indicates a degraded DOM proportion

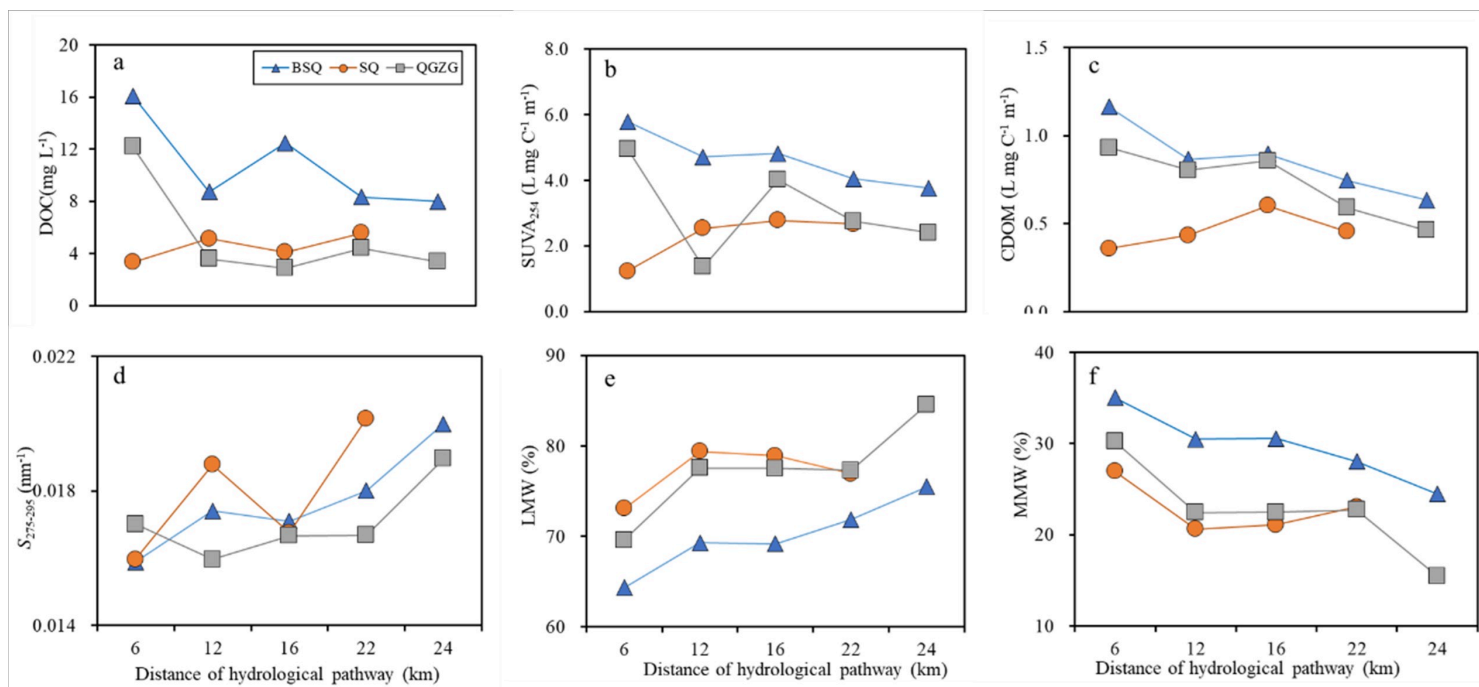


Figure 6

The changes of DOC concentration (a), SUVA₂₅₄ (b), CDOM (c), the values of S₂₇₅₋₂₉₅ (d), LMW DOM (e), and MMW DOM (f) along the fluvial pathways with distance from the headwater

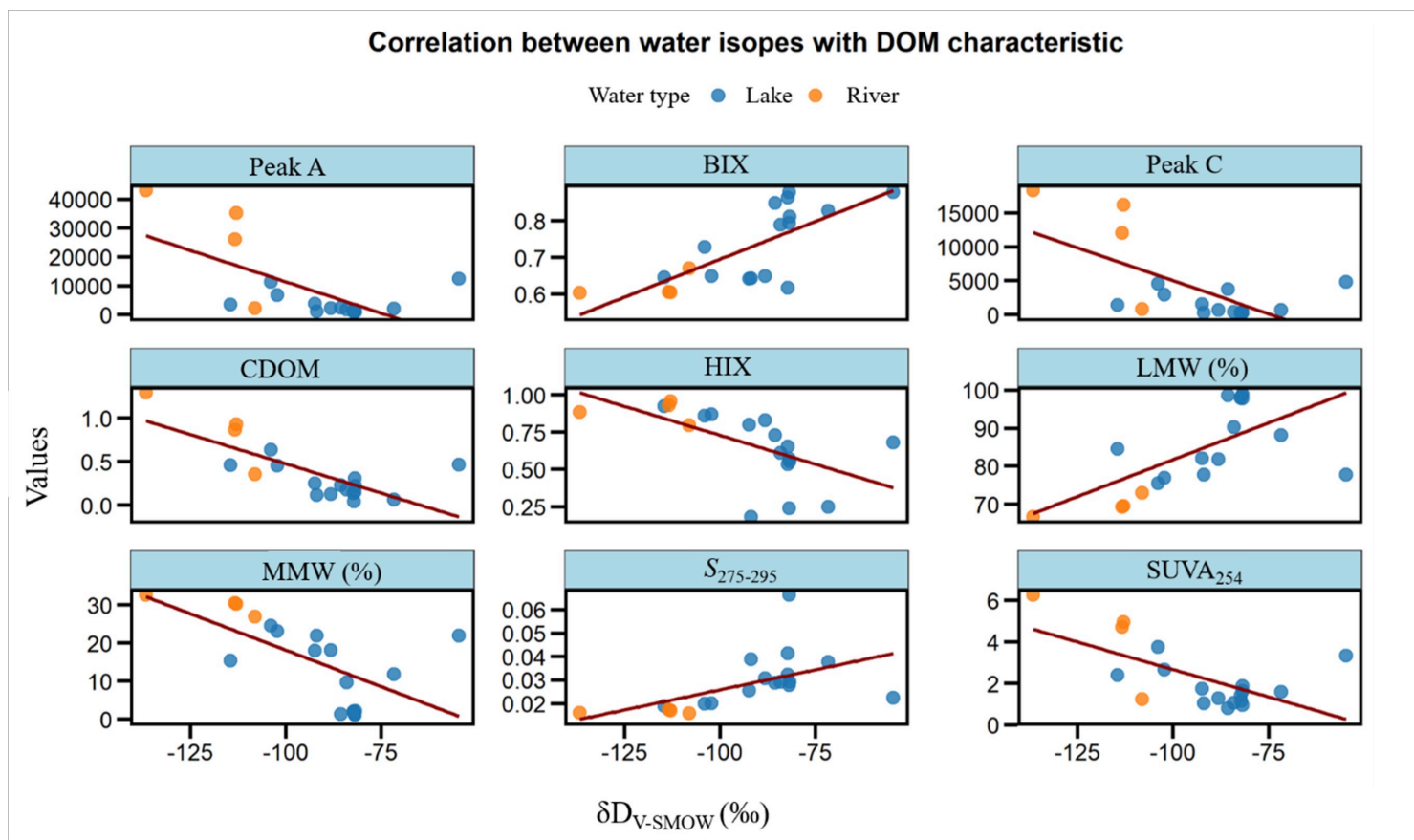


Figure 7

Spearman correlation between water isotope with DOM characteristic

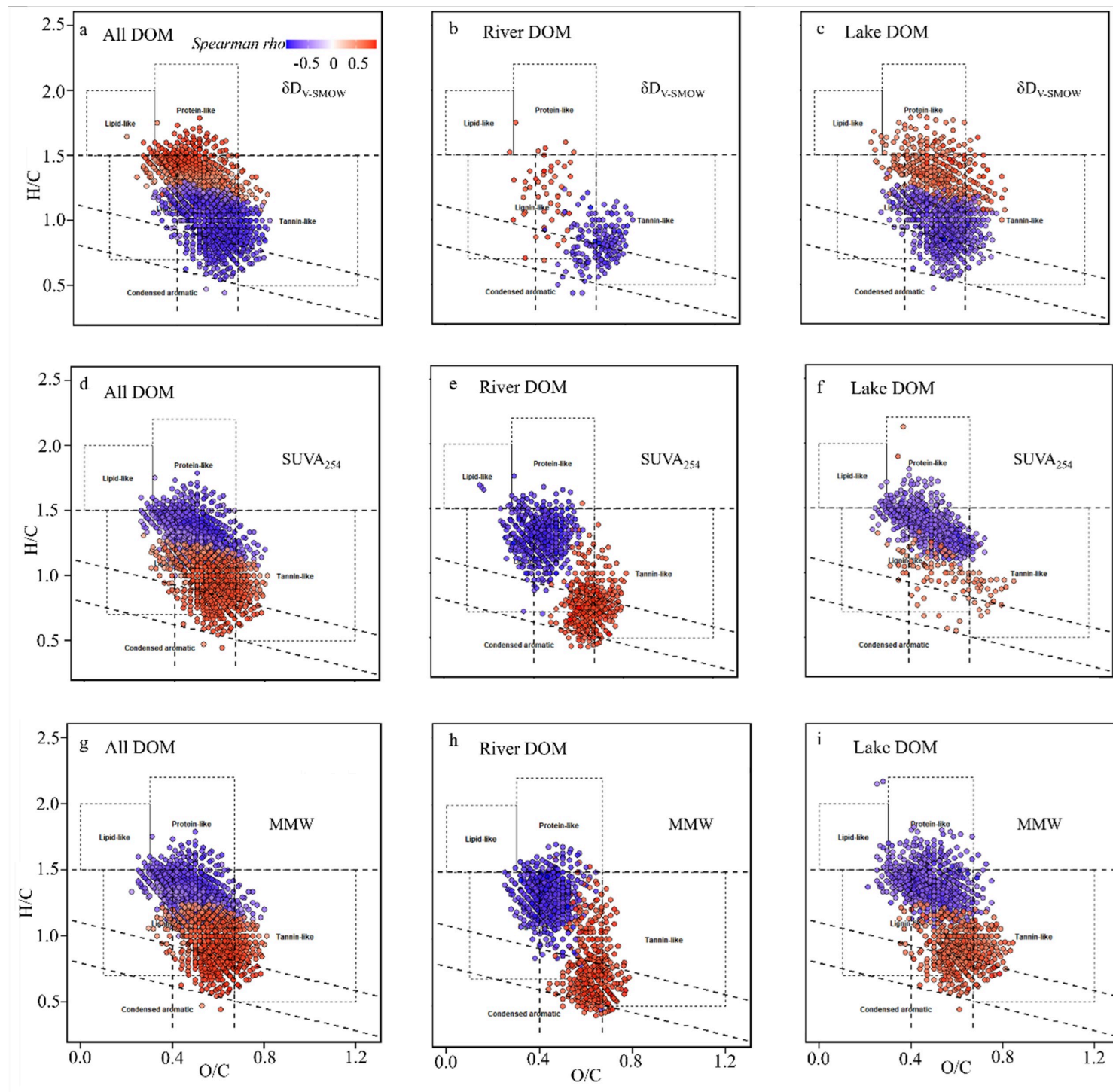


Figure 8

Spearman rank correlations between molecular composition as detected by FT-ICR MS in all collected samples, river and lake DOM, respectively and (a, b, c) water isotope (δD_{V-SMOW}), (d, e, f) the specific ultraviolet absorbance at 254 nm ($SUVA_{254}$), and (g, h, i) medium-molecular-weight (MMW) DOM. Red colors related to positive correlations; blue colors correspond to negative correlations

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