



1 **Spatiotemporal Shifts in Organic Carbon Sources in Cascade Reservoirs - a case study**
2 **in the Lancang River**

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22 ABSTRACT

23 Dam construction profoundly alters sediment organic matter regimes in large rivers. Yet,
24 the underlying mechanisms and how cascade reservoirs jointly shape organic matter sources
25 remain insufficiently understood. Here, we quantified organic matter sources across five
26 cascade reservoirs in the middle–lower Lancang River using stable isotopes with a Bayesian
27 mixing model. We found that algal-derived organic matter dominated during the dry season
28 and in reservoirs with longer retention, whereas terrestrial organic matter prevailed during the
29 wet season and intensified downstream with increasing watershed inputs. The structural
30 equation model analyses demonstrated that reservoir regulation and seasonality influenced
31 organic matter sources indirectly through nutrient dynamics rather than through direct
32 hydrological forcing. Hydrodynamic conditions, represented by a composite index derived
33 from hydraulic retention time and backwater length, were positively associated with nutrient
34 enrichment in both water and sediments, whereas temperature showed a negative relationship
35 with sediment nutrients; these nutrient variations were further linked to increased contributions
36 of terrestrial, algal, and sewage-derived organic matter. Complementary boosted regression
37 tree analyses further identified the key environmental predictors shaping organic matter
38 partitioning. Water temperature together with sediment nutrients formed the core controls on
39 the balance between terrestrial and algal organic matter (>48% cumulative influence).
40 Hydrodynamic factors were crucial for sewage-derived organic matter, with water depth and
41 retention time jointly contributing 35.2% of its variability. Together, these results reveal that
42 organic matter provenance in cascade systems emerges from the coupled effects of reservoir-



43 induced nutrient regulation and temperature–hydrology interactions, producing source
44 dynamics distinct from single-reservoir systems. This study provides mechanistic insights
45 needed to improve reservoir ecosystem management and underscores the importance of
46 integrating cascade-scale nutrient regulation into future assessments of human impacts on
47 riverine carbon cycling.

48 **Keywords:** Sediment organic matter, isotope, biogeochemical cycling, the Lancang River,
49 cascade reservoirs

50 **Introduction**

51 Large river systems are central to the global carbon cycle, functioning as both longitudinal
52 conduits for organic matter (OM) and active biogeochemical reactors that determine its
53 ultimate fate (Cole et al. 2007, Maavara et al. 2017, Chen et al. 2024). Central to these dynamics
54 are riverine sediments, which function as dual sinks and sources of organic carbon (OC)
55 through complex processes of deposition, sequestration, transformation, and emission
56 (Aufdenkampe et al. 2011, Mendonça et al. 2017). The composition and provenance of
57 sedimentary organic matter (SOM) ultimately dictate carbon burial efficiency and carbon
58 emission fluxes. Therefore, fingerprinting OC sources is fundamental to understanding
59 ecosystem-scale carbon turnover and evaluating the ecological ramifications of hydropower
60 development on the global carbon cycle (Tranvik et al. 2009, Raymond et al. 2013, Gao et al.
61 2021).



62 The proliferation of dams has fundamentally restructured riverine carbon cycling
63 (Maavara et al. 2017, Maavara et al. 2020, Dethier et al. 2022). By reducing flow velocities
64 and extending hydraulic residence time (HRT), dam construction enhances particle settling,
65 thereby altering the transport and burial patterns of land-derived organic matter. Concurrently,
66 increased water depth triggers thermal stratification and alters light availability, which in turn
67 shifts the balance between allochthonous organic matter inputs and in-reservoir primary
68 production (Mendonça et al. 2017, Tranvik et al. 2018, Schulz-Zunkel et al. 2022). In cascade
69 reservoir systems, these impacts are not merely localized but accumulate along the river
70 continuum, where sequential reservoirs synergistically reshape hydrodynamics, sediment
71 trapping efficiency, and nutrient stoichiometry (Li et al. 2020, Maavara et al. 2020, Wang et al.
72 2024). Collectively, these dam-induced modifications are expected to exert profound controls
73 on both the magnitude and proportional contributions of organic matter inputs to the benthos.

74 However, the interplay between dam-induced alterations and natural hydrological
75 seasonality creates a complex spatiotemporal mosaic of carbon processing (Chen et al. 2015,
76 Xu et al. 2023). In large monsoonal rivers like the Lancang River, pronounced seasonal shifts
77 in discharge and sediment loads further complicate these dynamics. While the impacts of
78 individual impoundments are well-documented, the collective influence of multi-reservoir
79 cascades, where sequential reservoirs may either amplify or attenuate watershed signals,
80 remains an area of significant uncertainty. Specifically, how these "serial discontinuities"
81 mediate the balance between allochthonous inputs and autochthonous production under
82 contrasting hydrological regimes is yet to be mechanistically elucidated. Addressing this gap



83 is critical for moving beyond site-specific observations toward a basin-scale understanding of
84 carbon cycling in heavily regulated river networks (Raymond et al. 2013, Regnier et al. 2013,
85 Fang et al. 2023).

86 The objectives of this study were to: (1) quantify the relative contributions of multiple
87 sedimentary organic carbon (SOC) sources in cascade reservoirs using a stable isotope-based
88 mixing model, (2) identify the environmental drivers (e.g., HRT, nutrient availability, and
89 monsoonal discharge) underlying spatial and seasonal variability of SOC sources, and (3)
90 evaluate the implications of cascade hydropower development for longitudinal carbon
91 connectivity. By integrating hydrological and operational context, this study provides new
92 insights into how cascade dams modulate SOC dynamics in river systems.

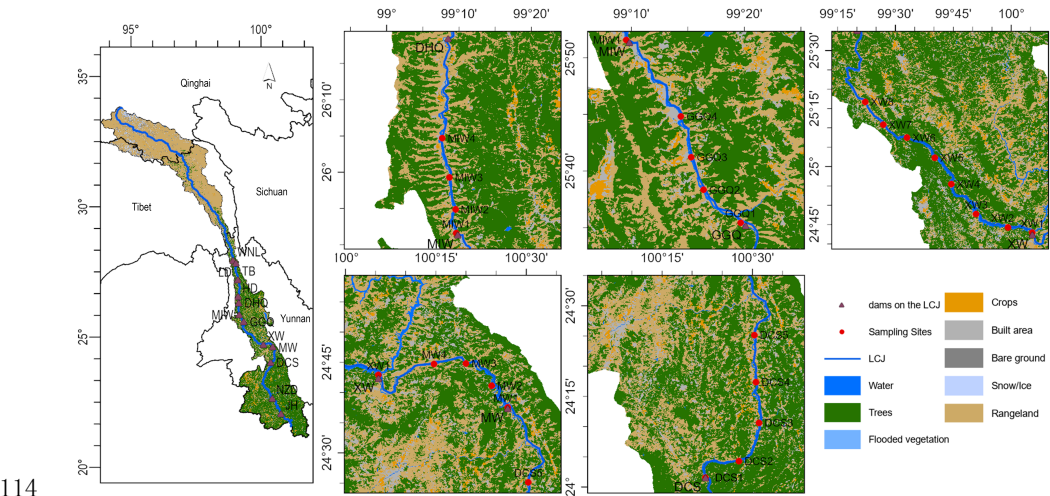
93 **2. Materials and Methods**

94 **2.1 Study Area**

95 The Lancang River, the upper reach of the Mekong, traverses the Tibetan Plateau and
96 Yunnan Province in China before cascading into Southeast Asia. Its steep topographic relief
97 has made it one of the world's most concentrated regions for hydropower development, with
98 the middle and lower reaches hosting a series of intensive damming projects. This study focuses
99 on a representative cascade segment spanning from the Miaowei (MIW) to the Dachaoshan
100 (DCS) reservoirs (Fig.1). These impoundments exhibit distinctive hydrodynamic regimes and
101 HRT, with their specific morphometric and operational characteristics summarized in Table
102 S1.



103 The basin is governed by a pronounced monsoonal climate, with 80%–85% of annual
104 precipitation occurring during the wet season (May–October). This hydrological seasonality
105 triggers pulsed fluctuations in river discharge and sediment transport (Shi et al. 2020, Zhou et
106 al. 2024). Land-use patterns vary along the cascade continuum; generally, vegetation richness
107 increases progressively from upstream to downstream reaches, following the descending
108 altitudinal gradient (Lang et al. 2024, Zhang et al. 2025). Furthermore, localized anthropogenic
109 and natural stressors differentiate these reservoirs: the Manwan (MW) reservoir is heavily
110 impacted by intensive aquaculture and fishing activities, while the Gongguoqiao (GGQ)
111 reservoir receives perennial input from a turbid tributary characterized by severe upstream soil
112 erosion. Collectively, these diverse conditions provide a unique natural gradient to investigate
113 the impact of cascade damming on the sources and dynamics of SOC.



114 **Fig.1** Sampling locations in Lancang River including five major reservoirs (Miaowei (MIW),
115 Gongguoqiao (GGQ), Xiaowan (XW), Manwan (MW), Dachaoshan (DCS))

117 **2.2 Sampling Design**



Field campaigns were conducted in September 2023 and April 2024, capturing the peak of the wet season (high water level) and the dry season (low water level), respectively. Samples were taken in both the lacustrine zones (from boats) and the fluvial zones (from bridges or riverbanks). At each site, in situ physicochemical parameters, including pH, water temperature (WT), dissolved oxygen (DO) and electrical conductivity, were measured using a calibrated multiparameter probe (YSI, Yellow Springs, OH, USA). Surface water samples (250 mL) were collected in pre-cleaned polyethylene bottles, stored in the dark, frozen, and transported to the laboratory. Water samples were analyzed for total phosphorus (wTP), total nitrogen (wTN), water nitrate (wNO_3^- -N), water nitrite (wNO_2^- -N), and water ammonium (wNH_4^+ -N) using a spectrophotometer (DR6000, Hach, USA) following the National Standards of China (2002). The water total carbon (wTC) concentrations in water samples were measured using a TOC analyzer (Multi N/C 3100, Analytik Jena GmbH, Germany).

Surface sediments (0–20 cm) were collected using an Ekman grab sampler (ZG0204, Shanghai ZiGui Instrument Co., Ltd.). After removal of coarse debris (e.g., rocks, branches), samples were homogenized and immediately frozen with liquid nitrogen. In the laboratory, sediments were freeze-dried and analyzed for total carbon (TC) content using an elemental analyzer (Vario MACRO cube, Elementar Inc., Germany). Sediment total phosphorus (sTP), sediment total nitrogen (sTN), sediment nitrate (sNO_3^- -N), sediment nitrite (sNO_2^- -N), and sediment ammonium (sNH_4^+ -N) concentrations were determined spectrophotometrically (DR6000, Hach, USA).

2.3 Stable isotope analysis and three-end-member mixing model (TEMM)



139 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of sediment organic matter were measured using an isotope ratio mass
140 spectrometer (IRMS) coupled to an elemental analyzer. Isotopic ratios were expressed in δ
141 notation relative to Vienna Pee Dee Belemnite (V-PDB) for carbon and atmospheric N_2 for
142 nitrogen:

$$143 \quad \delta X(\text{‰}) = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 \quad (1)$$

144 where X is ^{13}C or ^{15}N , and R is the corresponding heavy-to-light isotope ratio ($^{13}\text{C}/^{12}\text{C}$ or
145 $^{15}\text{N}/^{14}\text{N}$) (Middelburg and Nieuwenhuize 1998, Torres et al. 2012).

146 To quantify the sources of SOM in the Lancang River cascade, we employed a Bayesian
147 three-end-member mixing model using the MixSIAR package in R (Stock and Semmens 2016,
148 Stock et al. 2018, Choi et al. 2025). Based on the hydro-ecological setting of the basin and
149 previous in situ data from regional field surveys (Wang et al. 2019, Bao et al. 2025), three
150 primary potential sources were defined: (1) Terrestrial organic matter (T-OM): Derived from
151 upstream riverine inputs, riparian vegetation, and soil erosion from the Tibetan Plateau and
152 adjacent catchments; (2) Autochthonous Algae organic matter (A-OM): Generated via in-
153 reservoir phytoplankton and periphyton primary production; (3) Sewage-derived organic
154 matter (Sew-OM): Representing anthropogenic inputs, including domestic wastewater and
155 agricultural runoff.

156 The end-member isotopic signatures were determined using an integrated approach that
157 combines published literature ranges with constraints derived from the measured isotopic
158 compositions of sediment samples in this study (Table S2). This strategy was adopted to better
159 represent the specific hydro-biogeochemical conditions of the Lancang River cascade, which



160 differ from those of typical river–lake systems. T-OM was characterized by relatively depleted
161 $\delta^{13}\text{C}$ values ($-27.8 \pm 2.0\text{‰}$) and moderate $\delta^{15}\text{N}$ values ($5.4 \pm 1.5\text{‰}$), consistent with inputs
162 from C_3 -dominated upstream soils, vegetation debris, and riverine particulate matter. A-OM
163 exhibited comparatively enriched $\delta^{13}\text{C}$ values ($-16.0 \pm 2.5\text{‰}$) and intermediate $\delta^{15}\text{N}$ values
164 ($6.0 \pm 1.5\text{‰}$), reflecting in-reservoir primary production under HRT. The relatively enriched
165 $\delta^{13}\text{C}$ signature of A-OM is consistent with the influence of a $\delta^{13}\text{C}$ -enriched dissolved inorganic
166 carbon pool in the carbonate-rich Lancang River basin. Sew-OM showed markedly enriched
167 $\delta^{13}\text{C}$ ($-4.5 \pm 2.5\text{‰}$) and elevated $\delta^{15}\text{N}$ values ($8.5 \pm 2.0\text{‰}$), indicative of anthropogenic inputs
168 associated with wastewater discharge and intensified nitrogen cycling. The enriched carbon
169 signature may also be related to contributions from C_4 -based agricultural runoff (e.g.,
170 sugarcane and maize) in the midstream catchment (Yang et al. 2025, Yin et al. 2025).

171 Notably, these end-member values deviate from commonly reported ranges, particularly for
172 algal and sewage sources. Such deviations likely reflect the distinctive environmental setting
173 of the Lancang River cascade, characterized by strong hydrological regulation, high-altitude
174 catchment inputs, and altered carbon and nitrogen cycling processes. The selected signatures
175 are constrained by the observed isotopic distribution of sediment samples, ensuring that the
176 mixing space adequately encompasses the empirical data. Sensitivity analyses further
177 demonstrated that the end-member configuration yields stable and robust estimates of organic
178 matter contributions across both seasons and reservoirs.

179 In the MixSIAR framework, "Reservoir" was treated as a fixed effect to capture spatial
180 patterns across the cascade while accounting for internal variability. The model was run using



181 a "long" MCMC chain (300,000 iterations) to ensure convergence, which was verified using
182 Gelman-Rubin and Geweke diagnostics. Posterior means and 95% credible intervals are
183 reported for each source at the reservoir scale (Gelman and Shalizi 2013). Additionally, site-
184 specific contributions were evaluated independently to capture localized heterogeneity,
185 considering process error (Parnell et al. 2010). Due to differences in model structure, reservoir-
186 level estimates may not equal the arithmetic mean of site-level estimates (Gelman and Hill
187 2007). We acknowledge that these estimates are relative and reflect inherent uncertainties in
188 end-member characterization; thus, results are interpreted as indicative of broad ecological
189 trends (Link and Barker 2009a, b).

190 **2.4 Statistical Analyses**

191 All statistical calculations were performed using R software. Seasonal and spatial
192 differences among reservoirs were assessed using two-way ANOVA followed by Tukey's
193 HSD post hoc tests, with a significance threshold of $p < 0.05$. Data visualization was conducted
194 using Origin 2024. The correlation analysis between SOC sources and hydro-environmental
195 parameters was based on simple linear regression after data normalization. The Bayesian
196 mixing approach (using the MixSIAR package) was performed in R 4.1. Composite indices
197 were derived from variables of the same type (e.g., hydro-index, water and sediment nutrient
198 variables) using principal component analysis (PCA) to reduce dimensionality and mitigate
199 multicollinearity. Based on these indices, a structural equation model (SEM) was constructed
200 using the R plspm package to assess the direct and indirect effects of environmental factors on
201 water and sediment nutrients and the proportion of allochthonous organic matter. Model



evaluation included bootstrap significance of path coefficients, as well as latent variable average variance extracted (AVE) and overall goodness-of-fit (GoF).

3. Results

3.1 Environmental conditions along the cascade

Monitoring of five cascade reservoirs from the wet season (Autumn 2023) to the dry season (Spring 2024) revealed significant spatiotemporal variations in key environmental parameters (Fig.2). WT peaked in the wet season (maximum 26.57°C in XW Reservoir), exhibiting a significant negative correlation with DO concentrations, which were highest in the dry season. pH values were consistently higher in the wet season than in the dry season.

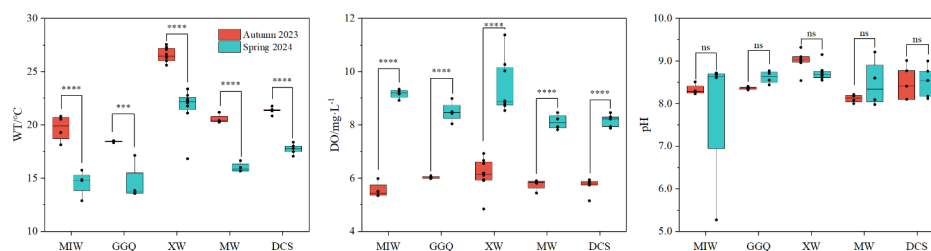
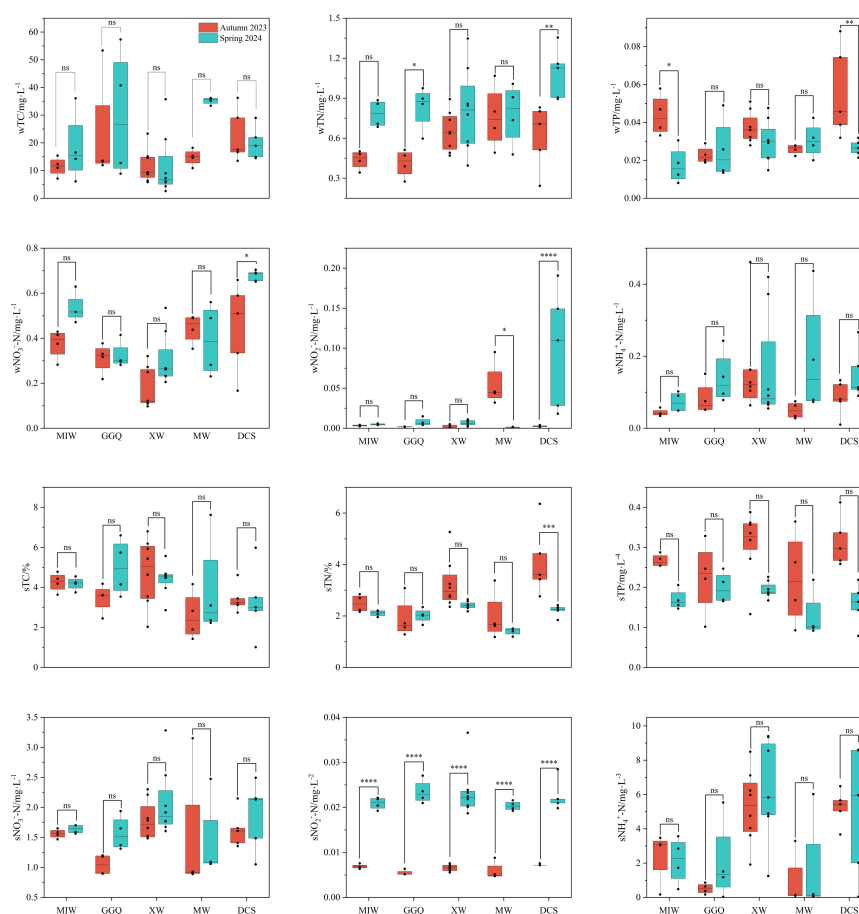


Fig.2 Longitudinal variations in water temperature (WT), dissolved oxygen (DO), and pH of surface waters along the Lancang River, from MIW to DCS (following the flow direction).

Fig.3 illustrates the variations in nutrient concentrations in surface water and sediment samples. The highest average TC contents in both water and sediments were observed in GGQ Reservoir during the dry season. wTN generally showed higher average values in the dry season of 2024 than in the wet season of 2023; both wTN and sTN exhibited significant seasonal differences at the DCS site. In contrast, average concentrations of water and sediment total phosphorus were predominantly higher in wet season of 2023 than in dry season of 2024.



220 Regarding nitrogen species, both water and sediment compartments displayed a cumulative
221 effect from upstream to downstream. Additionally, $w\text{NO}_2^-$ -N and $s\text{NO}_2^-$ -N demonstrated
222 significant seasonal variations (ANOVA, $p < 0.05$). Notably, the significant accumulation of
223 $s\text{NO}_2^-$ -N during the dry season indicates intense N transformation activities at the sediment-
224 water interface and a high potential for internal release in the cascade reservoirs during this
225 season.



226



227 **Fig.3** Longitudinal variations in nutrient concentrations in surface water and sediments along
228 the Lancang River, from MIW to DCS (following the flow direction). Parameters include
229 total carbon (TC), total nitrogen (TN), total phosphorus (TP), nitrate (NO_3^- -N), nitrite (NO_2^- -
230 N), and ammonium (NH_4^+ -N) for both water (w) and sediment (s) compartments.

231 **3.2 Characteristics of sediment $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ variations**

232 The stable carbon and nitrogen isotopic compositions ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of surface
233 sediments across the five cascade reservoirs exhibited pronounced spatiotemporal
234 heterogeneity (Fig.4). Overall, $\delta^{13}\text{C}$ values fluctuated within a wide range of -24.9‰ to -1.7‰,
235 while $\delta^{15}\text{N}$ values varied between 1.9‰ and 9.0‰.

236 Spatially, the most depleted $\delta^{13}\text{C}$ signatures were recorded in the downstream DCS
237 reservoir, with values ranging from -24.9‰ to -17.2‰. In contrast, the MW and GGQ
238 reservoirs displayed significantly more enriched $\delta^{13}\text{C}$ values (MW: -18.8‰ to -2.5‰; GGQ: -
239 18.9‰ to -3.6‰). Regarding nitrogen isotopes, the GGQ and DCS reservoirs were
240 characterized by relatively elevated $\delta^{15}\text{N}$ values, reaching up to 9.0‰ and 8.4‰, respectively.
241 Conversely, the MW reservoir exhibited the lowest $\delta^{15}\text{N}$ levels, falling to a minimum of 1.9‰.
242 Two-way ANOVA results further confirmed that both the reservoir factor and the season factor
243 exerted significant influences on the isotopic signatures of both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ ($p < 0.05$).

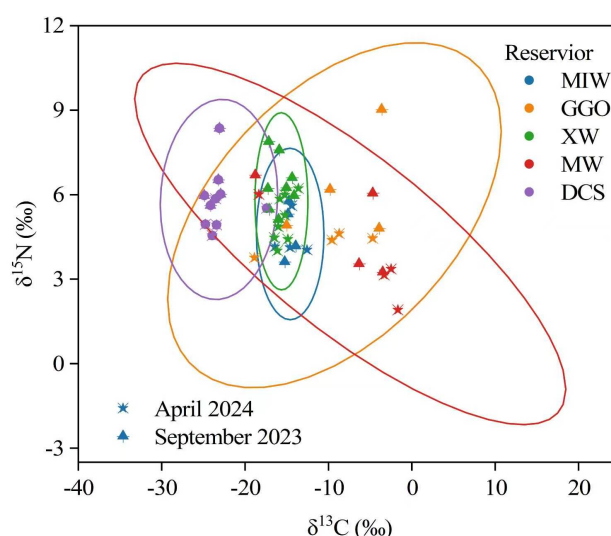


Fig.4 End-member diagram of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of sedimentary organic matter from cascade reservoirs in the middle and lower reaches of the Lancang River

3.3 Spatial and seasonal variations in SOC source contributions

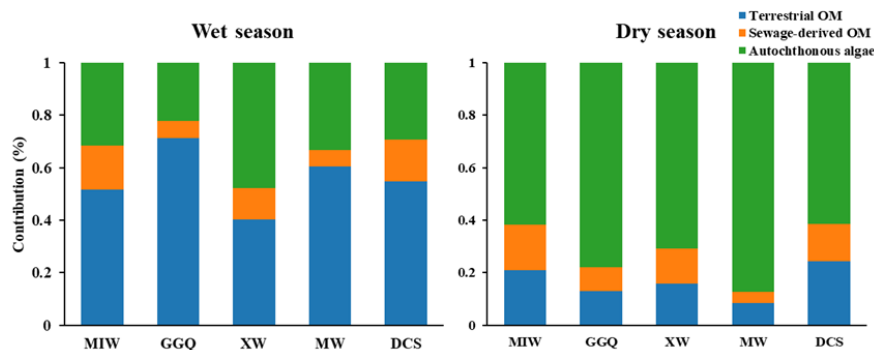
The three-endmember mixing model revealed pronounced spatiotemporal shifts in the provenance of SOM across the five cascade reservoirs (Fig.5). Overall, the contribution of Sew-OM was relatively minor, accounting for only 4.5%–17.3% of the total SOM.

During the wet season, T-OM constituted a major portion of the SOM across all reservoirs. The highest T-OM contributions were recorded in the GGQ (71.2%), MW (60.3%), DCS (54.9%), and MIW (51.5%) reservoirs. Notably, even in the XW reservoir, where the terrestrial proportion was the lowest (40.2%), T-OM still constituted nearly half of the total SOC.

In stark contrast, a dramatic shift in source composition occurred during the dry season (April 2024), with autochthonous algae becoming the primary contributor, ranging from 61.3% to 87.2%. This algal dominance peaked in the MW reservoir at 87.2%. Concurrently, the



258 contribution of T-OM experienced a sharp decline to between 8.3% and 24.3%, reaching its
259 minimum in the MW reservoir (8.3%).



260
261 **Fig.5** Contributions of different sources to sedimentary organic matter from cascade
262 reservoirs in the middle and lower reaches of the Lancang River

263 3.4 Relationships between environmental factors and SOM source contributions

264 The integrated Mantel test and Pearson correlation analysis (Fig.6) elucidate the complex
265 cascade of interactions between hydrological regulation, environmental gradients, and SOM
266 sources. Hydrological factors, including hydraulic retention time (HRT), length of backwater
267 area (LBA), and water depth (WD), exhibited strong correlations with water-column and
268 sedimentary physicochemical properties rather than directly with OM sources. Specifically,
269 HRT, LBA, and WD were significantly positively correlated with WT and $\text{sNH}_4^+\text{-N}$. Both HRT
270 and LBA also showed significant positive links with $\text{wNO}_3^-\text{-N}$, while LBA further exhibited
271 strong positive correlations with pH, wTC and sTN. Additionally, WD was uniquely associated
272 with elevated $\text{wNH}_4^+\text{-N}$.

273 Within the internal network of physicochemical variables, several key parameters
274 emerged as direct predictors of OM provenance. WT, DO, and wTN, along with sediment



properties such as sTP and sNO₂⁻-N, demonstrated highly significant correlations with the contributions of A-OM and T-OM. These correlations underscore a mechanism where hydrological regulation alters the thermal and nutrient regimes of the cascade reservoirs, which in turn acts as the proximal driver for the shift between autochthonous primary production and terrestrial detritus accumulation.

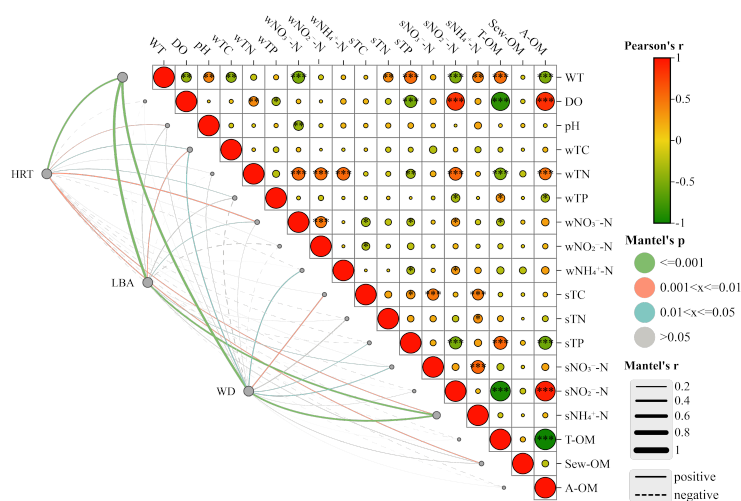


Fig.6 Integrated Mantel test and correlation heatmap showing the relationships between hydrological factors, environmental variables, and sediment organic matter (OM) sources in the Lancang River cascade reservoirs. The left panel presents Mantel test results, illustrating the correlations between hydrological indices, water depth (WD), hydraulic retention time (HRT), and length of backwater area (LBA), and grouped environmental variables as well as OM source contributions. Line thickness indicates the magnitude of correlation strength. Solid lines represent positive correlations, while dashed lines represent negative correlations. Line color reflects statistical significance: green for highly significant relationships, and gray for non-significant relationships. The right panel displays the Pearson correlation matrix



among water physicochemical parameters (e.g., WT, DO, pH, nutrients), sediment properties (e.g., sTC, sTN, sTP), and OM source contributions (T-OM, Sew-OM, and A-OM indicating terrestrial, sewage-derived, and algal OM, respectively). Color gradients represent correlation coefficients (from -1 to $+1$), with warmer colors indicating positive correlations and cooler colors indicating negative correlations. Asterisks denote statistical significance ($*p < 0.05$, $**p < 0.01$).

To further elucidate the direct and indirect influences of reservoir regulation and nutrient dynamics on OM provenance, an SEM was employed (Fig.7). The results indicated that reservoir and seasonal disparities primarily modulate OM contributions through indirect nutrient regulation. Specifically, hydrological indicators exerted significant positive effects on nutrient pools in both the water column and sediments, while WT had a significant negative impact on sedimentary nutrients. In turn, sedimentary nutrients significantly and positively influenced the contributions of T-OM, A-OM, and Sew-OM. These findings suggest that reservoir regulation and seasonal shifts do not directly alter OM provenance; instead, they operate by restructuring nutrient dynamics within the water–sediment continuum.

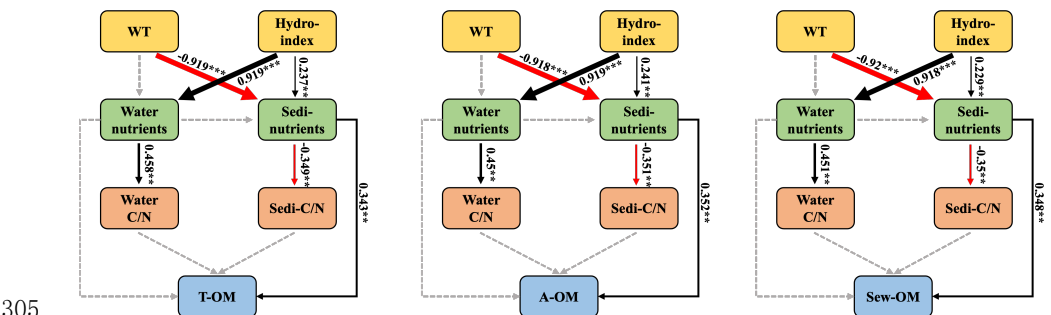
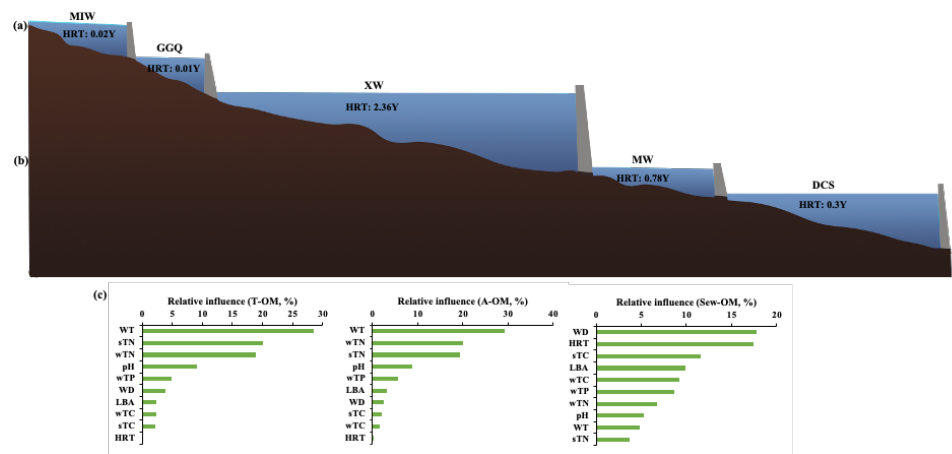


Fig.7 The factors regulating the sediment organic carbon source contribution. In the structural equation model (SEM) analysis, black arrows represent significant positive pathways, red



arrows represent significant negative pathways, and gray dashed arrows indicate nonsignificant pathways. Values next to the arrows represent standardized effect sizes with statistical significance ($*P < 0.05$; $**P < 0.01$; $***P < 0.001$). The Hydro-index variable in the SEM represents the first component from the principal component analysis (PCA) conducted with the HRT and the LBA data; water and sediment nutrients indicate the first component from the PCA conducted with the TC, total nitrogen and the total phosphorus content of water and sediment samples, respectively; Water C/N and sedi-C/N represent the ratios of TC to nitrogen content in water and sediment, respectively. T-OM, A-OM and Sew-OM indicate the contributions of terrestrial, algal, and sewage-derived organic matter, respectively.

To complement the SEM-based path analysis, Boosted Regression Tree (BRT) models were utilized to quantify the relative importance of individual environmental factors in shaping SOC source contributions (Fig.8). Among all variables, WT and nitrogenous nutrients (wTN, sTN) emerged as the core environmental drivers governing the partitioning of terrestrial and algal inputs, with a cumulative relative influence exceeding 48%. Although HRT was positively correlated with the A-OM proportion, this relationship was not statistically significant (Fig.8c) and possessed limited explanatory power. Notably, for Sew-OM, hydrodynamic processes played a dominant role, with WD (17.7%) and HRT (17.5%) jointly controlling the spatial extent and dilution of point-source pollution (cumulative influence of 35.2%). sTC (11.5%) and wTC (9.2%) followed in importance, while WT showed relatively low explanatory power for A-OM.



329

330 **Fig.8** Conceptual diagram of the sources and impacts of sediment OM in the cascade
331 reservoirs in the middle and lower reaches of the Lancang River. (a) Conceptual Diagram of
332 Water Depth and Hydraulic Retention Time in a Cascade of Five Reservoirs; (b) The
333 relationships of the OM contribution of autochthonous algae and hydraulic residence time in
334 wet season and dry season. (c) The relative influences (%) of predictor variables in the
335 boosted regression tree model (BRT) for the OM source.

336 4. Discussion

337 4.1 Spatiotemporal heterogeneity of environmental drivers under cascade regulation

338 Our findings underscore the pronounced spatiotemporal variability of environmental
339 factors in cascade-regulated reservoirs, which fundamentally governs the provenance and
340 dynamics of SOM. WT exhibited a distinct seasonal pattern, exceeding 25°C during the wet
341 season (September) and decreasing to 13–18°C in the dry season. This thermal variation
342 corresponded with a shift in stratified conditions: warmer temperatures in the wet season
343 promoted thermal stratification and moderate oxygen depletion (approximately 5–6 mg L⁻¹),



344 whereas enhanced vertical mixing in the dry season elevated DO levels (approximately 8–11
345 mg L⁻¹, [Table.S3](#)). Such seasonal fluctuations are consistent with observations in other cascade
346 systems, where hydrological regimes modulate oxygen dynamics and nutrient cycling (Shi et
347 al. 2023, Yang et al. 2025). Seasonal precipitation and runoff pulses induced sharp fluctuations
348 in water total carbon (wTC). However, the timing and magnitude of these changes varied
349 among reservoirs due to differences in hydraulic regulation. In the dry season, extended HRT
350 and reduced flushing favored nutrient accumulation, particularly in inorganic nitrogen forms
351 (NO₃⁻-N, NH₄⁺-N). This pattern aligns with studies indicating that prolonged retention times
352 in cascade reservoirs can lead to increased nutrient concentrations and altered biogeochemical
353 processes (Ouyang et al. 2025, Zhang et al. 2025).

354 Sediment stoichiometry further reflected these seasonal differences. During the wet
355 season, lower carbon-to-nitrogen (C/N) ratios (approximately 1–2.5) and higher total nitrogen
356 (TN) and total phosphorus (TP) contents indicated enhanced deposition of nitrogen-rich
357 terrestrial material fueled by watershed inputs. In contrast, some reservoirs exhibited higher
358 C/N ratios in the dry season, accompanied by elevated NH₄⁺-N and NO₃⁻-N concentrations in
359 sediments, suggesting intensified organic matter mineralization and nitrogen cycling under
360 prolonged retention and stronger bottom–surface coupling (Schneider et al. 2010, Jiang et al.
361 2025). These findings are consistent with research demonstrating that sediment nutrient
362 dynamics in cascade reservoirs are influenced by both hydrological conditions and
363 anthropogenic activities (Kuriata-Potasznik et al. 2020, Szatten and Habel 2020).



364 Compared with natural lakes or single reservoirs, where HRT often emerges as the
365 primary control of organic matter dynamics, cascade systems exhibited more complex patterns
366 (Chen et al. 2020, Du et al. 2021). In our study, upstream reservoirs partially buffered terrestrial
367 inputs by trapping sediments and organic matter, while downstream reservoirs received both
368 attenuated upstream pulses and additional allochthonous inputs, leading to asynchronous
369 responses along the cascade. This cascade-induced stratification of hydrodynamic conditions
370 disrupted the direct and linear relationship between HRT and OM dynamics observed in single-
371 reservoir systems. Similar cascade effects have been reported in the Mekong and Yangtze River
372 basins, where cumulative regulation resulted in nutrient and carbon dynamics divergent from
373 those of individual reservoirs (Shi et al. 2017, Chen et al. 2024).

374 **4.2 Mechanisms of spatiotemporal variability in organic matter sources under reservoir** 375 **regulation**

376 The three-endmember mixing model, integrated with SEM and BRT analysis, elucidates
377 a sophisticated regime shift in the provenance of SOM across the Lancang cascade. Our SEM
378 results (Fig.7) suggest that the shift in SOM provenance is an indirect consequence of altered
379 nutrient stoichiometry and thermal stratification, which reorganize the biogeochemical
380 template of the water-sediment continuum.

381 Specifically, hydrological indicators (Hydro-index, representing HRT and LBA) exert
382 significant positive effects on nutrient pools in both the water column and sediments. During
383 the dry season, prolonged HRT transforms these reservoirs from mere transport conduits into
384 active biogeochemical reactors, favoring the proliferation of A-OM. The stoichiometric



385 composition of SOM provides further evidence for these seasonal dynamics. In the dry season,
386 A-OM exhibited relatively higher C/N ratios (Table.S2), which likely stems from the
387 preferential mineralization of nitrogen-rich labile components, leaving behind residual carbon-
388 rich refractory matter (Meyers 1994, Harning 2013). This interpretation is robustly supported
389 by the elevated concentrations of sedimentary NH_4^+ -N and NO_2^- -N observed during the dry
390 season, suggesting accelerated nitrogen cycling and intensified benthic-pelagic coupling under
391 prolonged retention (Kuypers et al. 2018).

392 Notably, this sedimentary signature is mirrored in the overlying water column, where
393 dissolved total nitrogen (DTN) concentrations in April (dry season) significantly exceeded
394 those in September (wet season), with more pronounced disparities in downstream reservoirs
395 (MW and DCS) compared to upstream sites (Table.S3). This consistency implies that the
396 mineralization of algal-derived OM serves as a secondary nitrogen source to the water column,
397 explaining the seasonal enrichment of DTN in the dry season (Liu 2018, Wang et al. 2021).
398 Such sediment-water coupling effects underscore how cascade damming exacerbates
399 spatiotemporal heterogeneity.

400 Contrary to conventional paradigms in isolated lakes where HRT is often the "master
401 variable" dictating OM dynamics (Zhang et al. 2023, Ouyang et al. 2025), our BRT analysis
402 reveals that HRT alone has limited explanatory power for the variance in OM provenance
403 (Fig.8). This deviation from traditional expectations can be attributed to the cascade cumulative
404 effect: upstream reservoirs intercept suspended sediments and attenuate terrestrial signals,
405 while downstream reservoirs integrate these attenuated fluxes with additional inputs from



406 tributary catchments and enhanced in situ production. This longitudinal feedback mechanism
407 breaks the simple linear relationship between HRT and OM composition typically found in
408 solitary lentic systems. Similar observations in the Mekong and Yangtze cascades confirm that
409 sequential damming significantly intensifies the spatial heterogeneity of nutrient and carbon
410 dynamics (Maavara et al. 2017, Chen et al. 2020, Maavara et al. 2020). Consequently, the
411 interplay of monsoonal "pulse-shunt" delivery in the wet season and the "biogeochemical
412 reactor" effect in the dry season, mediated by cascade-driven nutrient restructuring, defines the
413 modern carbon cycle of the Lancang River.

414 **4.3 Ecological Implications of Changes in Organic Carbon Inputs to Reservoirs**

415 The pronounced seasonal alternation between algal-dominated (dry season) and
416 terrestrial-dominated (wet season) OM reflects a sophisticated coupling of hydrological forcing
417 and biogeochemical responses. In the dry season, the synergistic combination of hydrodynamic
418 stability (prolonged HRT and expanded LBA) and favorable nutrient stoichiometry (e.g.,
419 elevated inorganic nitrogen and sTP) triggers a "biogeochemical reactor" effect, where
420 autochthonous production becomes the primary sedimentary carbon source. Conversely, the
421 wet season "pulse-shunt" mechanism flushes allochthonous soil organic carbon into the system,
422 effectively suppressing in situ primary production through physical scouring and reduced light
423 availability (Casas-Ruiz et al. 2020, Catalan et al. 2023).

424 Crucially, our study demonstrates that in the Lancang cascade, indirect nutrient-mediated
425 pathways supersede direct hydrodynamic variables as the proximal drivers of SOC dynamics.
426 While HRT is traditionally viewed as the "master variable" in isolated lakes, the cumulative



427 impacts of cascade regulation, characterized by inter-reservoir feedbacks and high-frequency
428 regulation, attenuate the singular influence of residence time. Instead, a “nutrient – thermal
429 filtering” mechanism emerges. As evidenced by our SEM, hydrological indicators (Hydro-
430 index) primarily act by restructuring nutrient pools, while WT exerts a strong negative
431 constraint on sedimentary nutrient retention.

432 This shift has significant ecological ramifications. As anthropogenic nutrient loading and
433 global warming intensify, the “algalization” of sedimentary carbon may escalate, particularly
434 in mid-stream sections like MW, where agricultural nutrient runoff further stimulates in situ
435 primary production. The accumulation of labile, algal-derived OM in these reservoirs creates
436 potential “biogeochemical hotspots” for mineralization. This process may accelerate
437 greenhouse gas emissions (e.g., CH₄ and CO₂), thereby complicating carbon-neutrality
438 strategies in regulated tropical and subtropical basins (Tranvik et al. 2009, Raymond et al. 2016,
439 Zhou et al. 2024).

440 **5 Conclusion**

441 This study provides a comprehensive assessment of SOC provenance and its
442 environmental drivers within a major monsoonal cascade reservoir system. Our findings reveal
443 that while seasonal climate variability establishes the baseline pattern of organic matter (OM)
444 succession, oscillating between allochthonous dominance in the wet season and autochthonous
445 dominance in the dry season, cascade regulation introduces a significant layer of
446 biogeochemical complexity. Integrated evidence from isotopic mixing models and sedimentary



stoichiometry confirms that the SOC pool is collectively governed by the interplay of watershed inputs, internal nutrient cycling, and thermal constraints.

Notably, the anomalously enriched $\delta^{13}\text{C}$ features observed in the mid-stream reservoirs (e.g., Manwan) underscore the substantial influence of local C_4 -based agricultural runoff and the enriched DIC pools characteristic of carbonate-rich basins. These site-specific findings highlight the inherent spatial heterogeneity of cascade systems and justify the calibration of end-member values based on regional hydrochemical contexts. Furthermore, this study challenges existing paradigms by demonstrating that nutrient-mediated and thermal drivers supersede direct hydraulic control (e.g., HRT) in modulating SOC dynamics. To fully elucidate the long-term fate and stability of this carbon, future research should integrate isotopic methods with molecular biomarkers and ^{14}C dating. These multidimensional insights are crucial for refining global carbon models and improving the ecological management of dam-dense river networks worldwide.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Availability of data and material

The datasets generated and/or analyzed during the current study are available from the corresponding author on reasonable request.



468 **Competing interests**

469 The authors declare that they have no competing interests.

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475 **Author contributions**

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477 analysis, Data curation. Xudong Zhou: Writing-review & editing, Methodology, Investigation.
478 Bingcan Jiang: Writing-review & editing, Visualization. Yuqing Lin: Writing-review & editing,
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480 Xingcheng Yan: Writing-review & editing, Supervision, Methodology, Funding acquisition,
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