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Extreme drought–accelerated dissolved carbon metabolism triggers pulsed CO_2 outgassing in karst lakes

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Abstract

Karst aquatic ecosystems are important reservoirs of dissolved carbon (C), supporting dynamic CO_2 fluxes through the biological C pump. However, our current understanding of how sophisticated interactions between aquatic microbiomes and dissolved C turnover constrain the timing of CO_2 sequestration and emission remains limited. Here we capture an extreme drought event and the ensuing relatively wet conditions from systematic investigations in karst lakes, demonstrating that temporally distinct microbiomes are tuned to the metabolic patterns of dissolved C and thereby modulate CO_2 emissions. Specifically, we find that the extreme drought accelerates respiration of dissolved organic C, sharply increasing the CO_2 evasion rate. Wet conditions stimulate photosynthetic uptake of dissolved inorganic C, consuming lake CO_2 while promoting labile organic C formation. We therefore propose that pulses of CO_2 emissions from karst lakes occur after wet conditions end, as a consequence of rapid remineralization of newly produced bioavailable organic C, especially during extreme droughts. Our findings highlight the crucial importance of managing periodic CO_2 outgassing from karst waters under drought conditions for the implementation of region-specific C neutrality strategies.

Keywords: Karst waters, aquatic microbiome, dissolved carbon, CO_2 flux, extreme drought

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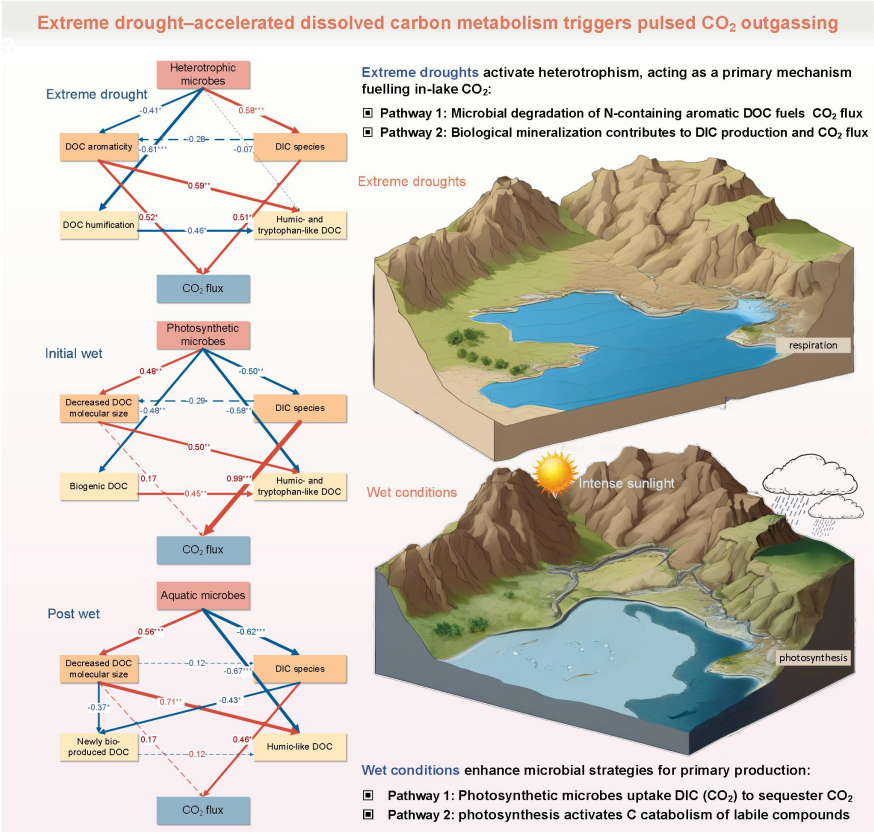
Graphical Abstract



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1. Introduction

Lakes store, metabolize and release large quantities of natural carbon (C), representing a funnel of aquatic C budget (Bogard et al., 2019; Borges et al., 2022; Evans et al., 2017). Therefore, there is mounting evidence that lakes function as "biogeochemical reactors", receiving terrestrial C and continuously cycling the bulk of aquatic C (Pi et al., 2022; Rodríguez-Cardona et al., 2023). Yet to date, the mechanisms driving lake C cycling are poorly understood, particularly regarding the underlying factors that constrain C emission (Chen et al., 2022; Mendonça et al., 2017). It is estimated that inland lakes, despite covering only ~3% of the land surface, contribute to 38% of aquatic C outgassing (Tranvik et al., 2009). Although the drivers of these emissions are regionally investigated (Maberly et al., 2013; Mu et al., 2023; Serikova et al., 2019), a fundamental factor governing C fixation, mineralization, and subsequent uptake or release remains elusive. Deciphering the cycling of dissolved C offers a promising avenue to address this knowledge gap, as it mediates C turnover between organic and inorganic forms and accounts for ~90% of the global C flux from terrestrial to aquatic ecosystems (Drake et al., 2020), making it essential for understanding aquatic C budget (Raymond and Hamilton, 2018; Song et al., 2018).

Evidence suggests that seasonal wetness and drought control the dynamics of dissolved inorganic C (DIC) concentrations and species (Rehn et al., 2023; Tye et al., 2022). These events also alter water-land connectivity and thus the export of dissolved organic C (DOC) to inland waters (Li et al., 2022a; Wang et al., 2024; Yuan et al.,

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2024). Subsequently, aquatic photosynthesis utilizes DIC, while heterotrophic respiration of DOC generates CO_2 (Guo et al., 2023; Leles and Levine, 2023). Consequently, dissolved C turnover and CO_2 emissions are anticipated to be highly interconnected through hydrological and biological mechanisms (Hu et al., 2022; Kellerman et al., 2014; Monteith et al., 2023). For example, experimental data suggest that droughts can stimulate dissolved C cycling by transiently accelerating primary production and, more persistently, DOC respiration (Harjung et al., 2019).

These pervasive turnover and emission of aquatic C, in particular, can be substantial in karst waters. The prevailing view suggests the regional specificity of karst regions, specifically with respect to ecological fragility and the significant role in carbonate C sink (Chen et al., 2023; D'Ettorre et al., 2024). Yet, recent reports also highlight significant dissolved C cycling and CO_2 sequestration in karst aquatic ecosystems, attributed to the “biological C pump” effect (He et al., 2024; Sun et al., 2022; Zhang et al., 2024). Carbonate weathering can couple with photosynthetic uptake of DIC, resulting in self-amplifying CO_2 sink during karst water cycle (Liu et al., 2018; Wang et al., 2022). Nevertheless, primary production may trigger DOC catabolism and rapid cycle of active C (Ni et al., 2023; Ni et al., 2022). These critical processes are associated with aquatic biology, but little is known about how lake microorganisms drive dissolved C turnover and ultimately modulate CO_2 emissions in karst lakes.

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Theoretically, microbiome is anticipated to govern internal cycling between DIC and DOC, and this process, in turn, may affect specific CO_2 pathways (Li et al., 2022b; Shangguan et al., 2024). Prior studies found significant DIC uptake by C-fixing microorganisms (Li et al., 2024) and recalcitrant DOC sequestration *via* heterotrophic bacteria in karst aquatic systems (He et al., 2022b; Xu et al., 2023), which potentially regulate CO_2 fixation and outgassing in response to specific pathways of C metabolism. Therefore, we hypothesized that microorganisms will interact with dissolved C to establish distinctive CO_2 drivers in karst lakes. To test this hypothesis, we conducted a two-year investigation, capturing an extreme drought event and its following rainfalls, with the aims of revealing: 1) temporal interactions of aquatic microbiome with dissolved C dynamics; 2) specific pathways governing karst lake CO_2 flux; and 3) microbially-driven dissolved C turnover and the resulting CO_2 emission or sequestration. Achieving these aims is expected to uncover the underlying mechanisms of C source-sink transformation in karst water environments, ultimately supporting efforts toward C neutrality.

2. Materials and methods

2.1. Study area

Observations were performed in the karst lakes Hongfeng (HFH), Laoma (LMH) and Baihua (BBH), located between 25º57′ to 26º42′N in latitude and 105º58′ to 106º34′E in longitude (Fig. 1). The catchment geology is predominantly karst lithology i.e., dolomite and limestone. Lake HFH and BHH, two of the largest artificial lakes in

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Guizhou Province, cover surface areas of 57.2 and 14.5 km^2, with water volumes of 6.01×10^8 and 1.91×10^8 m^3, respectively. As a segment of the Maotiao River, the LMH is supplied by several tributaries that connect Lake HFH to BHH. These karst waters are situated in a subtropical monsoon climate zone, with annual temperatures ranging from -7.8°C to 37.5°C. The wet season lasts from May to October, delivering an average annual precipitation of 1130 mm. Specifically, an extreme drought event occurred in 2022–2023, with monthly rainfall <10 mm during the drought (early winter), >100 mm during the initial-wet (early summer), and 50–100 mm during the post-wet (autumn) periods. These lakes acting as drinking water sources, are disrupted by agriculture and domestic sewage.

2.2. Fieldwork and laboratory analysis

During May to November from 2022 to 2023, our sampling captured an extreme drought event, allowing us to clearly identify the specific temporal scales during the drought, initial-wet and post-wet periods. Spatially, fieldworks were designed to incorporate full spectrum of the karst lakes from 32 sampling locations (Fig. 1a). Therefore, a total of 96 water samples were collected from our investigations. In details, we collected surface waters at a depth of ~10 cm and filtered them within 6 hours. Filtrates were stored in 1000-mL high-density polyethylene (HDPE) containers designed to eliminate headspace and air bubbles. Water samples were filtered using glass microfiber filters (Whatman, GF/F 47 mm, 0.7-μm) for dissolved C measurement, and polycarbonate membrane filters (Millipore, GF/F 47 mm, 0.22-μm)

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for microbial determination. Samples were refrigerated at 4°C during transport and stored at -70°C for microbiological analysis.

Water temperature and pH were *in-situ* determined with a portable pH meter (PHB-4, Shanghai). Wind velocity was measured using a Testo 410-1 anemometer (Testo, Germany). Total alkalinity was titrated with Alkalinity Test MColortestTM (Merck, Germany). DOC concentration was detected using varioTOC cube/select (Elementar, Germany). Chromophoric DOC was determined using a double-beam scanning spectrophotometer (UV-5500PC, Shanghai) with UV–visible absorption spectra ranging from 200 to 700 nm (1-nm interval). Fluorescence DOC was analysed using a RF-6000 Spectrophotometer (Shimadzu, Japan), with excitation and emission wavelengths of 200–450 (5-nm interval) nm and 250–600 nm (1-nm interval), respectively. Molecular DOC was characterized using Fourier transform ion cyclotron resonance mass spectrometry (FT-ICR MS). We combined equal volumes of water samples from each lake site, leaving us three composite samples for FT-ICR MS analysis. Details on sample pretreatment (solid-phase extraction, SPE) for FT-ICR MS are available in Supplementary Text S1.

Genomic DNA in sampling waters was extracted using E.Z.N.A. Water DNA Kit (OMEGA, USA) according to the manufacturers' instructions, and detected with 1% agarose gel electrophoresis. It employed universal primers 341F (5'-CCTAYGGGRBGCASCAG-3') and 806R

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(5'-GGACTACNNGGGTATCTAAT-3') for amplifying the V3–V4 hypervariable region of 16S rRNA, with a GeneAmp PCR System 9700 (ABI GeneAmp, USA). The PCR products were extracted by 2% agarose gel electrophoresis, and recovered from AXYPREP DNA Gel Recovery Kit (Axygen Biosciences, USA) with Tris-HCl for elution. Purified amplicons were pooled in equimolar and sequenced using paired-end on an Illumina MiSeq PE300 (Illumina, USA) following standard protocols.

2.3. Data processing and calculation

In this study, we employed a carbonate equilibria-based method for estimating aqueous DIC, using combinations of water chemistry parameters (pH, water temperature and total alkalinity) through CO_2SYS program (Xu et al., 2017). This program outputs concentrations of DIC species i.e., total DIC, HCO_3^-, CO_3^{2-} and dissolved CO_2, as well as aqueous partial pressure of CO_2 (pCO_2), a crucial indication for potential CO_2 emissions from aquatic environments. The following thin boundary layer model was used to calculate areal CO_2 flux (mmol m^{-2} d^{-1}) from the karst waters.

$$Areal\ CO_2\ flux = (pCO_{2water} - pCO_{2ir}) \times k \times K_h \quad (1)$$

This model proposes that the difference between aqueous (pCO_{2water}, μatm) and atmospheric pCO_2 (pCO_{2air}, μatm) can characterize the impetus and direction for CO_2 transfer. Temporal shifts in *in-situ* atmospheric CO_2 levels (dimensionally convertible to pCO_{2air}) are available in Fig. S1. By contrast, gas transfer velocity (k, m d^{-1}) can

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constrain the velocity of water-air CO_2 exchange, which is calibrated from normalized gas transfer velocity (k_{600}, cm h^{-1}) using water temperature and Schmidt number. Specifically, k or k_{600} serves as a function of water turbulence, empirically modelled by wind velocity in lakes and lentic rivers. Henry's constant (K_h, mmol m^{-3} μatm^{-1}) calibrated from *in-situ* temperature and pressure, characterizes CO_2 equilibrium at water-air interfaces. Details for chemical calculations of DIC species and thin boundary layer model see Supplementary Text S2.

We analysed UV–visible and fluorescent spectroscopy for understanding DOC component, origin and fate. Specifically, DOC-normalized absorption coefficient $SUVA_{254}$ (L mg^{-1} m^{-1}), an indicator of DOC aromaticity, was computed as the absorption coefficient (a_{254}, m^{-1}) divided by DOC concentration (mg L^{-1}). Spectral slope $S_{275\text{-}295}$, a proxy for DOC relative molecular weight, was calculated by nonlinearly fitting an exponential function to the absorption spectrum from 275 to 295 nm. Fluorescence index (FI) increases with intensified biological activity, and indicates allochthonous (< 1.4) and autochthonous (> 1.9) inputs for aquatic DOC, which was calculated as the ratio of emission intensity at 470 nm to 520 nm with an excitation of 370 nm. Biological index (BIX), a proxy for freshness of biologically produced DOC, was calculated as the ratio of emission intensity at 380 nm to 430 nm, using an excitation of 310 nm. Humification index (HIX), characterizing to DOC humification and biodegradability, was expressed as the ratio of total emission intensities at 435–480 nm divided by 300–345 nm, at an excitation of 254 nm. Parallel

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factor analysis (PARAFAC) was used to identify primary DOC component by separating excitation-emission matrices into independent fluorophores. The PARAFAC modelling employed residual and split-half analyses for component selection and correspondence validation.

FT-ICR MS analysis was conducted to examine dissolved organic matter (DOM, represents the specific material form of the general DOC) composition using a molecular formula calculator based on criteria with elemental combinations of $C_{0\text{-}\infty}H_{0\text{-}\infty}O_{0\text{-}\infty}N_{0\text{–}1}S_{0\text{-}1}$. Peaks were detected within S/N >4 and a mass accuracy of ≤ ±1 ppm. Van Krevelen diagrams plotting H/C against O/C were employed to visualize FT-ICR MS data. Seven DOM compositions were extracted based on the elemental ratios of H/C and O/C (Ni et al., 2024), involving carbohydrates, amino-sugars, saturated compounds, tannins, lignin, unsaturated hydrocarbons and condensed aromatic structures. The elements (C, H, O, N, P and S), and formulas (CHO, CHOS, CHON, CHOP, CHONS, CHONP, CHOSP and CHONSP) were identified based on molecular exact mass and matched against a molecular formulas database (Yan et al., 2024). The modified aromaticity index (AI-mod) and nominal oxidation state of carbon (NOSC) were calculated as follows:

$$AI\_mod = \frac{1 + \mathrm{C} - \frac{1}{2}O - S - \frac{1}{2}(N + H)}{\mathrm{C} - \frac{1}{2}O - N - S} \quad (2)$$

$$NOSC = \frac{4\mathrm{C} + \mathrm{H} - 3\mathrm{N} - 2\mathrm{O} - 2\mathrm{S}}{\mathrm{C}} \quad (3)$$

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Alpha diversity, calculated using Mothur (https://mothur.org/wiki/calculators/), was used to assess microbial community through the indices Coverage (community coverage), Chao (community richness) and Shannon (community diversity). We analysed microbial community and its relative abundance, ranking the top 20 microorganisms at genus level. Using Tax4Fun, we converted 16S into prokaryotic classification profiles in the KEGG database, enabling KEGG functional annotation for 16S RNA gene sequences. It provides insights into potential microbial functions based on their composition and abundance in aquatic environments, and specifically presents information on KEGG Orthology in this study.

2.4. Quality control

Water collection and analysis followed the standard procedures, as proposed by the American Public Health Association (1985). The pH probe was calibrated with 6.86 and 9.18 pH standard solution at 25℃, ensuring ±0.01 pH unit accuracy. Water temperature and wind velocity were accurate to ±0.5℃ and ± (0.2 m/s + 2% of measurements), respectively. Alkalinity Test MColortestTM measured total alkalinity with < 3% uncertainty. DIC species calculated from water chemistry may be overestimated due to non-carbonate alkalinity (Liu et al., 2020). We specifically assessed that non-carbonate alkalinity from nitrogen, phosphorus and organic C can result in a maximum 29.5% overestimation of DIC species. Consequently, we corrected this overestimation by using measured DIC concentrations (Fig. S2), which

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converted systematic errors into instrument errors (< 2%) for all DIC datasets. UV measurements were 10% replicated, suggesting an uncertainty of < 2 %. The inner filter effect of fluorescence data can be neglected since absorbances at 254 nm were all below 0.3 (Ohno, 2002). Excitation-emission matrices were corrected for Raman and Rayleigh scatterings through interpolation, and fluorescence intensity (A.U.) was normalized to Raman Unit (R.U.) *via* water Raman peak areas (Ni et al., 2024). FT-ICR MS and microbial analysis were conducted by China National Analytical Centre (Guangzhou, China) and Majorbio Bio-Pharm Technology Co. Ltd. (Shanghai, China), respectively.

2.5. Statistical analysis

Normality and homogeneity of variance were assessed using Kolmogorov-Smirnov test and Levene's test, respectively. Variables were log-transformed as needed to ensure normality assumptions. One-way analysis of variance (ANOVA) with Tukey HSD post hoc was employed to evaluate statistical differences across DIC species, DOC compositions and microbial variables. Correlation analysis was used to assess possible associations within or between dissolved C, CO_2 flux and microbial variables. We introduced a structural equation model (SEM) to examine how aquatic microorganisms interact with dissolved C and ultimately influence CO_2 flux through both direct and indirect pathways. We initially excluded the variables with nonlinear relationships (e.g., alpha diversity and Tax4Fun) to derive comparable standardized path coefficients. We further established and specified 6 latent variables according to

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the loadings of their associated observed variables (see Supplementary Text S3). In the SEM, we hypothesized that 1) photosynthetic and heterotrophic microbes will preferentially associate with DIC for anabolism and DOC for catabolism, respectively; and 2) dissolved C dynamics and CO_2 flux are intertwined due to carbonate chemistry, biogenic, and terrestrial regulations. The SEM with partial least squares path modelling was performed using the plspm package in R (Version 4.1.3). Statistical analyses and figures preparing were conducted using and OriginPro 2024 and MATLAB 2018.

3. Results

3.1. DIC species and CO_2 emissions

The significant carbonate kinetics in karst waters present an opportunity to understand the dynamics of aqueous DIC species. This study captured strong seasonality in water chemistry (Table 1), particularly with lower pH and water temperature during the extreme-drought period ($p < 0.001$ by ANOVA). *In-situ* measured total alkalinity (range: 2178.7–6210.8 μeq L^{-1}), along with DIC (range: 1538.7–6206.0 μmol L^{-1}) and HCO_3^- (range: 918.4–5970.6 μmol L^{-1}), had no temporal variations across the periods ($p > 0.05$). Extreme drought caused lower aqueous CO_3^{2-} but higher dissolved CO_2 levels in comparison to wet conditions ($p < 0.001$, Fig. S3). It should be noted that we corrected concentrations of DIC species by eliminating systematic errors from non-carbonate alkalinity, reducing average uncertainties of 6.8% for DIC, 7.0% for HCO_3^-, and 38.7% for dissolved CO_2 (Fig. S2).

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To estimate potential CO_2 emissions from the study lakes, we calculated aqueous pCO_2, k and areal CO_2 flux (Fig. 1). These lakes had a broad range of aqueous pCO_2 levels, spanning from 20 to 13479 μatm across sampling locations (Fig. 1b). We found that extreme drought (4437 ± 3468 μatm) unexpectedly caused a ~five-fold increase in mean pCO_2 relative to initial- (804 ± 1080 μatm) and post-wet periods (928 ± 1728 μatm, $p < 0.001$), which can escalate to ~ten-fold when considering median pCO_2 (Fig. 1b). Indeed, our dataset reveals that 61% of samples were oversaturated with CO_2 relative to atmospheric equilibrium (Fig. S1), attributable to high pCO_2 levels during extreme droughts. Gas transfer velocity k showed no significant temporal shifts ($p > 0.05$), ranging from 0.37–2.28 m d^{-1} with a mean of 0.62 ± 0.26 m d^{-1} (Fig. 1c). This is slightly lower than previously reported global average of 0.74 m d^{-1} from a similar empirical model based on wind speed (Raymond et al., 2013). We estimated areal CO_2 flux to be 42 ± 79 mmol m^{-2} d^{-1} (range: -24–459 mmol m^{-2} d^{-1}) from the karst lakes. However, it is also noted that the bulk of samples during wet periods were undersaturated (Fig. 1d). We show that extreme drought increased areal CO_2 efflux sharply (111 ± 104 mmol m^{-2} d^{-1}), relative to initial- (6 ± 22 mmol m^{-2} d^{-1}) and post-wet periods (10 ± 26 mmol m^{-2} d^{-1}) ($p < 0.001$). Our findings, therefore, may partially deviate from the previous understanding of aquatic karst carbon sinks (An et al., 2015; Binet et al., 2020; Liu et al., 2010), indicating that karst lakes could be a significant source of CO_2 driven by extreme drought events.

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3.2. DOC composition, origin and fate

We used spectroscopic and molecular methods to assess DOC composition, origin and fate (Fig. 2 and 3). Aqueous DOC concentrations had a ~30-fold variation (range: 0.76–22.1 mg L^{-1}) across the samplings (Fig. 2a). Extreme drought apparently elevated DOC concentrations to an average of 12.4 ± 3.7 mg L^{-1}, relative to initial- (5.4 ± 2.3 mg L^{-1}) and post-wet periods (5.7 ± 1.6 mg L^{-1}) ($p < 0.001$). DOC aromaticity descended significantly across the periods, with initial-wet > post-wet > extreme drought ($p < 0.01$), as suggested by $SUVA_{254}$. By contrast, relative molecular weight of DOC, indicated by $S_{275\text{-}295}$, was higher during extreme-drought period than wet periods ($p < 0.05$). We were able to identify DOC fluorescent component through PARAFAC, demonstrating two distinct humic-like (C1) and one tryptophan-like DOC (C2) across the periods (Fig. 2b). The temporal abundances differed significantly ($p < 0.001$), with %C1 > %C2 during the extreme drought yet %C1 < %C2 during wet conditions (Fig. S4). These karst waters received both allochthonous and autochthonous inputs, with 80% of samples falling within the FI range of 1.4–1.9 (Fig. 2c). As suggested by BIX, we found biologically produced young DOC was more abundant during initial-wet than extreme-drought period ($p < 0.05$). However, DOC humification proxied by HIX was notably greater during the extreme drought than that in the wet conditions ($p < 0.01$).

It captured the molecular formulas for a total of 8060, 8636 and 8403 FT-ICR-MS compounds in lake LMH, HFH and BHH, respectively (Fig. 3). The

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molecular formulas were classified into distinct categories based on H/C and O/C distributions, as well as exact mass in van Krevelen Diagram (Fig. 3a). The study lakes showed a similar range of DOM exact mass, varying from 114.031694 to 1121.181055 Da. We suggest that these lakes were governed by low-molecular-weight DOM, with 80%, 74%, and 77% of the detected molecules for LMH, HFH, and BHH having an exact mass < 500 Da, respectively. The summed intensity was highly variable for each DOM molecular category, notably with lignin compounds (or carboxy-rich acyclic molecules) comprising 83%–84%, followed by saturated compounds at 11%–13% across lakes. Amino-sugars also represented a notable 1.8%–2.3%, while carbohydrate, tannins, unsaturated hydrocarbons and condensed aromatic structures each occupied ≤ 1% across all molecular categories. These DOM molecules were largely comprised of atomic groups CHO (44.8%–49.2%), CHOS (17.2%–25.5%), CHON (19.2%–26.6%) and CHONS (5.6%–6.3%) (Fig. 3b). Each karst lake shared a comparable average AI_{mod} across FT-ICR-MS compounds ($p > 0.05$), while NOSC was higher in lake BHH (-0.29 ± 0.48) than that in LHM (-0.32 ± 0.48) ($p < 0.01$, Fig. 3c).

3.3. Aquatic microbiome in the karst lakes

To evaluate microbial processes in the karst lakes, we examined temporal variability of microbiome from 89 samples (Fig. 4). For the microbial diversity, a total of 121–351 ASV (14382 sequences), 236–479 ASV (40251 sequences) and 143-445 ASV (42507 sequences) were assigned during the extreme-drought, initial-wet and post-wet

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periods, respectively (Fig. S5). Rainfall increased microbial richness and diversity in the aquatic environment (Fig. 4a), as indicated by Chao (initial wet > post wet > extreme drought, $p < 0.05$) and Shannon (initial wet > post wet and extreme drought, $p < 0.05$). However, microbial coverage was higher in the extreme-drought period ($p < 0.01$). The top 3 microorganisms were *Acinetobacter*, *CL500-29_marine_group* and *Cyanobium_PCC-6307* at genus level, with the average relative abundances of 11.6% ± 10.3%, 10.3% ± 5.58% and 5.68% ± 3.91%, respectively (Fig. 4b). *Acinetobacter* and *CL500-29_marine_group*, important for C catabolism, had increased relative abundance during the extreme drought. By contrast, photosynthetic microorganisms *Cyanobium_PCC-6307* and *g_norank_f__norank_o__Chloroplast* were more abundant during the initial-wet period (Fig. 4b). Therefore, we found that amino acid catabolism was significant under extreme droughts, while carbohydrate anabolism was predominant under wet conditions (Fig. 4c, $p < 0.001$).

4. Discussion

4.1. Temporal interactions of aquatic microbiome with dissolved C dynamics

Karst aquatic ecosystems, with rapid kinetics of carbonate chemistry and biological metabolism involved, may develop associated strategies for dissolved C turnover (He et al., 2024; Ni et al., 2023; Xi et al., 2024). Here, our results show the consistent shifts of dissolved C with aquatic microbiome in karst lakes. Extreme droughts, for instance, set the stage for substantial proliferation of heterotrophic microbes (Fig. 4b) and thus microbial degradation of enriched DOC (Fig. 2a). As labile DOC is

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exhausted, these microbes are compelled to metabolize typically more refractory DOC. This aligns with recent observations in karst and thermokarst lakes (Hu et al., 2023; Ni et al., 2022), as also evidenced by the parallel increase in CO_2 levels (Fig. 1b) and decrease in DOC aromaticity (Fig. 2a), suggesting that in-lake aromatic compounds are partially labile during extreme droughts. By analysing DOC molecular composition, we specifically found that N-containing, rather than S-containing aromatics are more bioavailable for heterotrophic microorganisms (Fig. S6 and Supplement table S1).

Rainfall accelerates atmospheric CO_2 uptake and CO_3^{2-} generation in karst aquatic environments (Zhao et al., 2024), which, combined with photosynthetic uptake of DIC, provides conditions for the enhancement of photosynthetic microorganisms (Fig. 4b). This explains the consistently low CO_2 levels during wet periods (Fig. 1b), aside from the known dilution effect (Ni et al., 2019). Here, we suggest that initial rainfall following extreme droughts substantially boosts microbial richness and diversity (Fig. 4a), possibly due to amplified terrestrial inputs and rejuvenated aquatic biology (Fig. S7). Moreover, we were able to examine the associations between DOC molecular compositions and microorganisms, revealing that photosynthetic microorganisms generate substantial quantities of biodegradable DOC e.g., carbohydrate and lipid-like compounds (Fig. S6 and Supplement table S1). Therefore, our results indicate season-specific microbial strategies for dissolved C metabolism in karst lakes.

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4.2. Specific pathways governing karst lake CO_2 flux

Microbiome-driven dissolved C turnover can further alter CO_2 dynamics, especially in lakes with long-term hydraulic retention and active biological processes (Lindström and Bergström, 2004). Our results show that the photosynthesis-driven associations between microbiome, dissolved C, and CO_2 flux emerged substantially during initial-wet periods (Fig. S8). Studies previously predicted self-amplifying photosynthesis driven by carbonate dissolution in karst waters (He et al., 2022a; Liu et al., 2010). Here, we present direct evidence that photosynthetic microorganisms dominate the microbial communities during the initial-wet period (Fig. 4b). Extreme drought, however, decouples the linkages between dissolved C and CO_2 flux from photosynthetic microorganisms. Respiration of DOC e.g., tryptophan-like component in turn fuels lake CO_2 during the extreme-drought period (Fig. S8). Our data allow us to extrapolate that amino acids, aliphatic compounds and small molecular organic acids serve as primary substrates driving CO_2 production and emissions in these lakes (Fig. 9 and Supplement table S1).

Using SEM, we clearly demonstrate the specific pathways governing lake CO_2 transfer across the periods (Fig. 5). Our observations reinforce that extreme droughts stimulate microbial metabolism of aromatic DOC and contribute to CO_2 outgassing from the study lakes (Fig. 5a). Nevertheless, it emerged an alternative C metabolism pathway during the initial-wet period (Fig. 5a): photosynthetic microorganisms

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constrain DIC species and subsequent CO_2 flux in lakes. This photosynthetic pathway persisted during the post-wet period, yet we found a specific pathway involving aquatic microbes that promotes a decrease in molecular size and subsequent increases in humic-like abundance (Fig. 5a). This observation aligns with a previous study in karst aquatic ecosystems (Xia et al., 2022), suggesting that intense photosynthesis produces labile compounds and subsequently activates the catabolism of DOC pool, ultimately resulting in the selective accumulation of recalcitrant compounds. These findings, complement prior evidence from biodegradation assays (Ni et al., 2022), providing a new insight into photosynthetic products triggering significant microbial activities and dissolved C turnover in karst lakes.

4.3. Implications for biologically driven C cycling in karst waters

Karst aquatic ecosystems typically represent strong interactions between microbial metabolism and dissolved C turnover, driven by the known “biological C pump” (Yi et al., 2021; Zhang et al., 2024). While the specific C sink from this mechanism is well-documented (Cao et al., 2018; Chen et al., 2023; Sun et al., 2021), the causes of periodic C evasion from karst waters are still questionable. In this study, we propose that extreme droughts yield large CO_2 emissions from the karst lakes, increasing >10 times on average relative to wet conditions (Fig. 1d). Droughts apparently accelerate heterotrophic respiration of DOC, acting as a primary mechanism fuelling in-lake CO_2. Drought-enriched heterotrophic microorganisms extensively deplete labile DOC, and even resort to metabolizing previously recognized recalcitrant compounds. Aromatic

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DOC, for instance, characterized by microbial resistance, has recently been reported to be activated through photochemistry (Hu et al., 2023). Here, our results demonstrate a clear mechanism by which microbial degradation of N-containing aromatic compounds contributes to C metabolism (Fig. S6), indicating that extreme droughts suppress biological C sink in karst lakes.

Wet conditions in karst lakes, in contrast, show a distinct pathway governed by aquatic photosynthesis (Fig. 5b), aligning with the prior theory regarding karst biological C sink (Liu et al., 2018). This stimulates a substantial uptake of CO_2 and thus limit lake C emission. Our observations provide direct evidence that photosynthetic microorganisms produce carbohydrates and promote the formation of lipid-like (Fig. S6) as well as other low-molecular-weight compounds (Fig. S8). These labile DOC quickly engage in subsequent biological processes, accelerating the proliferation of heterotrophic microorganisms. Our efforts to upscale this mechanism demonstrate a clear causality: 1) catabolism of photosynthetically derived labile DOC stimulates heterotrophic microorganism growth; 2) recalcitrant DOC accumulates relatively as heterotrophic respiration increases, even though aromatic compounds are partially utilized; 3) a priming effect is triggered, promoting both labile DOC mineralization to CO_2 and the sequestration of recalcitrant DOC. These findings highlight that biologically driven organic C turnover critically determine the CO_2 uptake or release in karst aquatic ecosystems.

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Overall, as we initially hypothesized, aquatic microbiome interacts with dissolved C dynamics, establishing the distinctive CO_2 driving mechanisms that particularly fluctuate with biochemical timing in karst lakes. It is anticipated that pulses of CO_2 emissions will occur after wet conditions end, particularly under drought conditions, as a result of rapid decay of photosynthetically derived organic C. Therefore, managing C sink in karst aquatic systems depends heavily on mitigating the sudden bursts of DOC respiration, especially the dramatic increased CO_2 release during extreme droughts. Our results indicate that wet conditions significantly enhance biological strategies for CO_2 uptake in karst aquatic ecosystems, highlighting the crucial role of mitigating climate change-induced droughts in strengthening karst C sink.

4. Conclusion

Karst lakes represent distinctive microbial pathways for dissolved C metabolism and subsequent CO_2 sequestration or emission. Here, we specifically reveal the temporal dynamics of CO_2 fluxes driven by periodic interactions between aquatic microbiome and dissolved C turnover in the study karst lakes. We show that extreme droughts accelerate the proliferation of heterotrophic microbes and thus rapid respiration of DOC, resulting in a sharp increase in CO_2 emissions. By contrast, wet conditions stimulate aquatic photosynthesis, which consumes DIC and sequesters CO_2 within the lakes. We highlight that exhausted DOC compels heterotrophic microorganisms to metabolize refractory N-containing aromatic compounds, while photosynthetic

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microorganisms promote the formation of labile DOC compounds. These specific microbial strategies indicate that pulsed CO_2 outgassing from karst lakes occurs after periods of high photosynthetic activity, with the magnitude being significantly amplified during extreme droughts. Therefore, we propose that managing periodic CO_2 outgassing, particularly during droughts, is essential for developing C neutrality in karst waters.

Code/Data availability

The full dataset used for the evaluation of this study is publicly available at https://figshare.com/s/7475752c5f7b19718199.

Declaration of Competing Interest

All authors agree this submission and the authors declare that there is no conflict of interests regarding the publication of this article

Author contributions

The project was conceived by M.N. and Z.K. M.N. directed and managed the study, as well as prepared the first draft of the manuscript. Z.K. collected and analysed samples, contributed to data interpretation and paper writing. G.Z. specified the experimental conditions and measured CO_2 data. W.L. specified the experimental conditions and contributed to CO_2 data analysis and interpretation. J.P. conceptualized dissolved carbon turnover in this study, and contributed to data interpretation and

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paper writing. J.C. and J.Z. and X.W. provided comments on the manuscript. All authors reviewed and contributed to the final manuscript.

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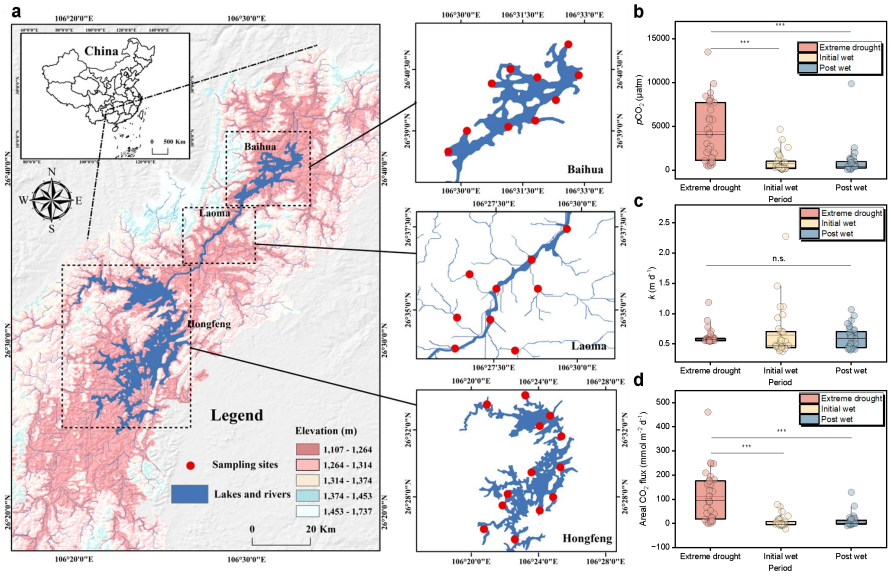

Fig. 1. Distribution of sampling locations and temporal patterns of CO_2 emissions in the karst lakes. (a) Map showing DEM information and observation sites. Variations of pCO_2 (b), k (c) and areal CO_2 flux (d) across extreme drought, initial wet and post wet periods. The boxes with bars represent 25%–75% percentiles with 5%–95% percentiles. Black lines, white lines and dots show median, mean and all data, respectively. Asterisks indicate statistical significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

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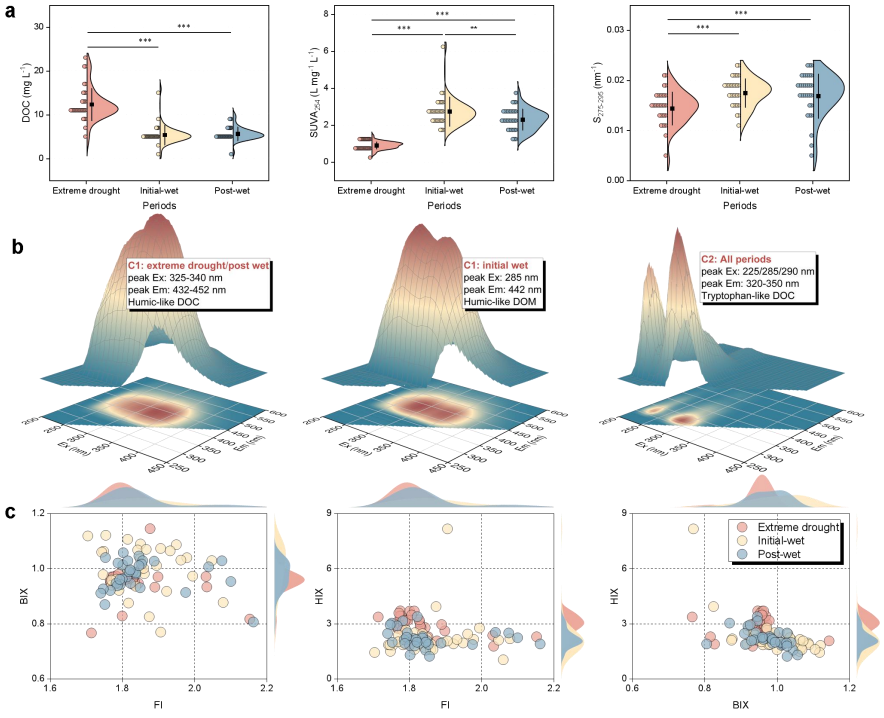

Fig. 2. Spectroscopic characteristics of DOC in the karst lakes. (a) Temporal patterns of DOC, $SUVA_{254}$ and $S_{275\text{-}295}$ over the study periods. Violins with dots represent Kernel Smooth distribution with all data. Black boxes with white bars show mean with standard deviation (s.d.). Asterisks indicate statistical significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. (b) 3D view of primary DOC fluorophores identified by PARAFAC analysis. (c) Distributions of FI, BIX and HIX over the study periods. Dots correspond to all data of these fluorescent parameters. The waves show Kernel Smooth distributions of the data.

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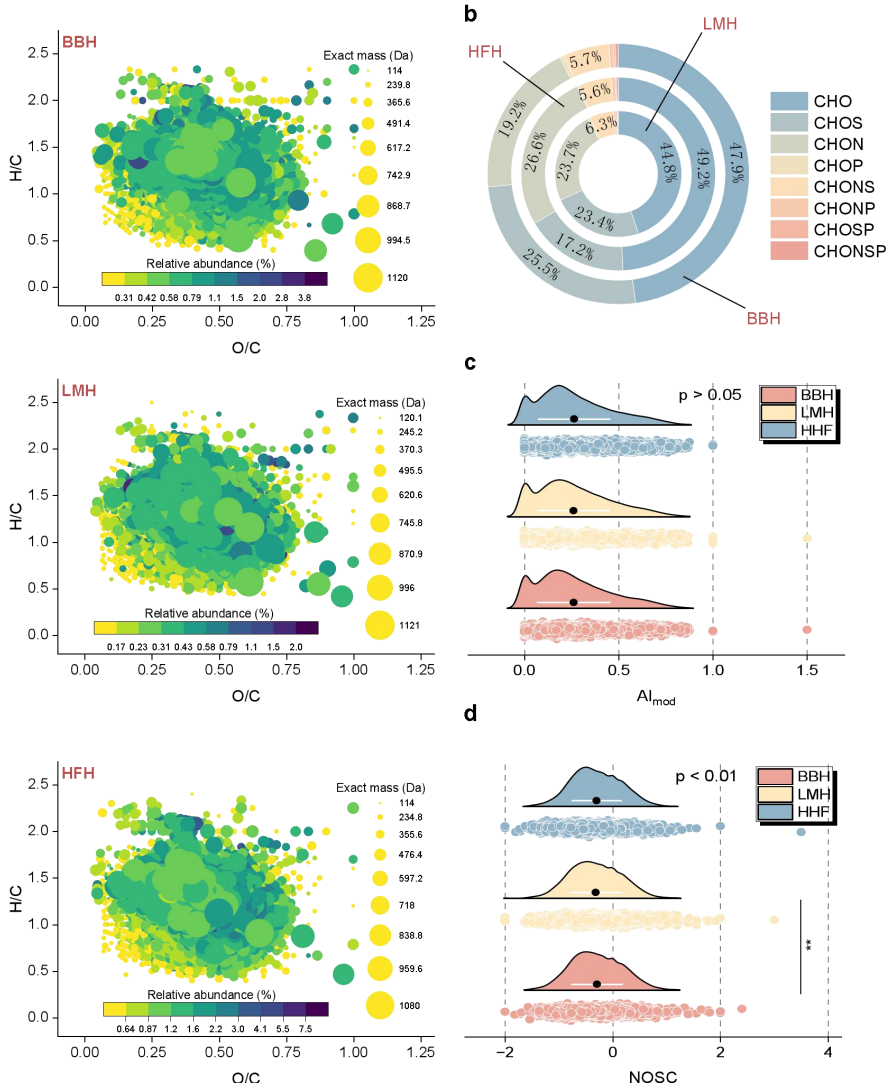

Fig. 3. Molecular characteristics of DOC in the karst lakes. (a) van Krevelen Diagrams plotting H/C against O/C with exact mass information of DOC molecules. (b) Proportions of primary DOC molecular formulas across the lakes. The AI-mod (c) and NOSC (d) across lakes. Violins with dots represent Kernel Smooth distribution with all data. Black spots with white bars show mean with standard deviation (s.d.).

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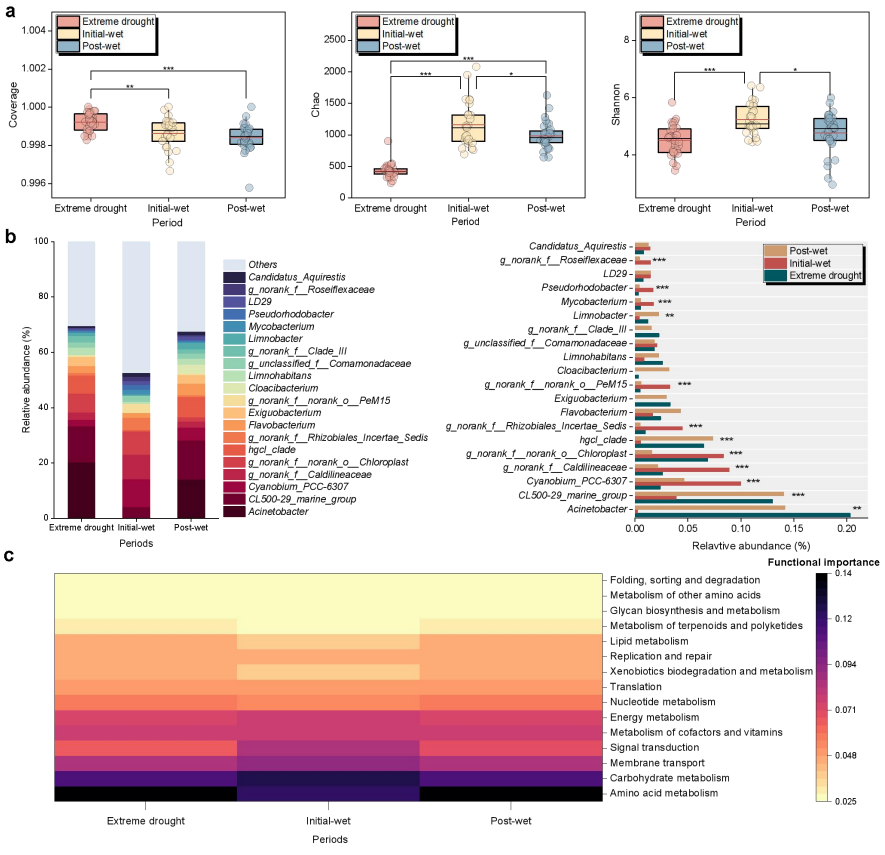

Fig. 4. Temporal variability of microbial communities and functions in the karst lakes. (a) Alpha diversity indices regarding Coverage, Chao and Shannon over the study periods. The boxes with bars represent 25%–75% percentiles with 5%–95% percentiles. Black lines, white lines and dots show median, mean and all data, respectively. Asterisks indicate statistical significance: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. (b) Comparison of the top 20 genera identified by relative abundance. (c) Potential microbial functions predicted by Tax4Fun based on the KEGG database.

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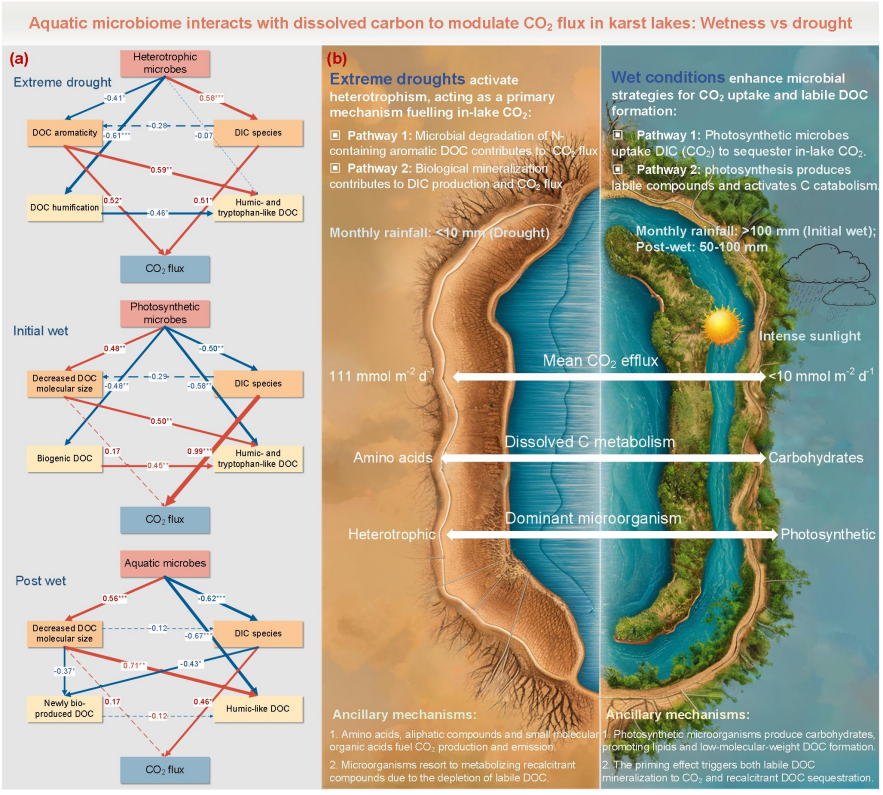

Fig. 5. Temporal pathways of aquatic microbiome-dissolved C interactions involved in CO_2 emission modulation in karst lakes. (a) The structural equation model showing temporal pathways of CO_2 flux driven by microbial communities and DIC-DOC turnover. Red and blue arrows represent positive and negative effects, respectively. Path coefficients are shown along the arrows. (b) A conceptual framework illustrating how microbiome interacts with dissolved carbon to modulate CO_2 emissions.

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Table 1. Temporal patterns of pH, water temperature, total alkalinity and DIC species in the karst lakes.

	n	Min	Max	Median	Mean	Std. Dev
Extreme drought						
pH	32	6.71	8.30	7.20	7.40	0.48
Water temperature (°C)	32	14.5	19.5	16.2	16.2	0.99
Total alkalinity (μeq L^{-1})	32	2325.7	4940.9	2726.5	2960.5	703.2
DIC (μmol L^{-1})	32	2405.0	5272.5	2828.5	3114.2	668.8
HCO_3^- (μmol L^{-1})	32	2290.3	4895.5	2645.1	2878.6	655.0
CO_3^{2-} (μmol L^{-1})	32	3.95	244.6	16.0	40.9	51.3
Dissolved CO_2 (μmol L^{-1})	32	18.0	602.4	177.0	194.7	153.5
Initial-wet						
pH	32	7.36	9.12	8.33	8.25	0.38
Water temperature (°C)	32	23.9	31.0	26.6	26.9	1.75
Total alkalinity (μeq L^{-1})	32	2178.7	6210.8	2895.3	3235.3	978.4
DIC (μmol L^{-1})	32	1538.7	6206.0	2688.8	3014.9	1042.5
HCO_3^- (μmol L^{-1})	32	918.4	5970.6	2428.0	2745.2	1073.0
CO_3^{2-} (μmol L^{-1})	32	35.7	752.7	218.2	243.5	155.1
Dissolved CO_2 (μmol L^{-1})	32	0.58	160.3	10.4	26.2	36.0
Post-wet						
pH	32	6.80	9.15	8.22	8.18	0.47
Water temperature (°C)	32	12.9	29.5	27.1	25.8	3.45
Total alkalinity (μeq L^{-1})	32	2239.7	5435.0	2795.5	3133.6	862.9
DIC (μmol L^{-1})	32	2096.8	5180.7	2576.5	2908.9	777.2
HCO_3^- (μmol L^{-1})	32	1546.7	4863.6	2441.5	2623.8	758.1
CO_3^{2-} (μmol L^{-1})	32	6.27	887.9	195.5	253.5	222.5
Dissolved CO_2 (μmol L^{-1})	32	1.04	315.9	14.3	31.6	57.1