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Sulfate-driven phosphorus recycling and the collapse of lacustrine ecological diversity in the mid-Triassic

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ABSTRACT

The Middle Triassic Ordos Basin witnessed the earliest rehabilitation of complex lacustrine ecosystems after the end-Permian mass extinction (EPME). The specific challenges faced by freshwater ecosystems during this interval remain unclear, however, owing to the limited spatiotemporal coverage of integrated biogeochemical studies. Here, we combine high-resolution geochronology, mineralogical and multi-proxy geochemical data from the mid-Triassic Ordos Basin with temporal and spatial biogeochemical modelling to reconstruct lake redox structure and nutrient dynamics. Our results indicate that a transient increase in external sulfate input strengthened endogenous phosphorus recycling and eutrophication, promoting shoaling and intensification of a metastable sulfidic zone at mid-depths. This shoaling would have led to poisoning of benthic habitats, causing a collapse of the oldest known Mesozoic lacustrine ecosystem. We propose that sulfate loading prolonged anoxia and ecological stress by extending the residence time of phosphorus, a mechanism that may be relevant to deoxygenation events and resulting biocrises in both ancient and modern lacustrine ecosystems.

Keywords: Mid-Triassic, lacustrine biocrisis, eutrophication, phosphorus recycling, biogeochemical modeling

1. Introduction

The end-Permian mass extinction (EPME, ca. 252 Ma) was a major biocrisis during which ~90% of marine species and ~70% of terrestrial vertebrate species went extinct, with environmental devastation from global wildfires, rapid warming and acid rain (Algeo and Shen, 2024). The Triassic witnessed a lengthy but non-contemporaneous reestablishment of both marine and terrestrial ecosystems, and marks the first major origin of modern ecosystems, sometimes referred to as the "Dawn of the Modern World" (Benton, 2010, 2016; Chen and Benton, 2012). Multiple fossil assemblages document a rapid re-establishment of trophically complex marine ecosystems in the Early and Middle Triassic (Dai et al., 2023; Roberts et al., 2025). In terrestrial non-aquatic ecosystems, many key modern vertebrates (e.g., dinosaurs and mammals) diversified rapidly (Fraser and Sues, 2011; Marsicano et al., 2016), and conifers and

cycadophytes radiated and established ecological dominance on land areas (Looy et al., 1999; Grauvogel-Stamm and Ash, 2005; Xu et al., 2025). By contrast, terrestrial aquatic ecosystems went through an interval of ca. 10 Myr without deposition of coal worldwide, termed the "Coal Gap" (Retallack et al., 2011), until the oldest known Mesozoic-type lacustrine ecosystem with multilevel trophic structures occurred in Member 7 of the Yanchang Formation (YC7) in the Ordos Basin, North China (Fig. 1). The YC7 interval, dated to ~242 Ma at the Anisian-Ladinian boundary, contains diverse fossil assemblages (e.g., chrysophyte cysts, insects and fish) (Yao et al., 2022; Zhao et al., 2020) and high concentrations of hydrocarbons (Qiu et al., 2015; Zhang et al., 2009) and redox-sensitive trace metals (e.g., U, Mo) (Du et al., 2019; Yuan et al., 2017).

Although the YC7 lagerstätte has been widely cited as evidence for the re-establishment of complex Middle Triassic lacustrine ecosystems, it did not continue to thrive through the mid-Triassic, and instead crashed within millions of years (Yao et al., 2022; Zhao et al., 2020), with the mechanisms responsible for its subsequent collapse remaining unresolved. Previous studies have ascribed the collapse to lethal microbial proliferation (Mays et al., 2021), episodic volcanism (Bian et al., 2025; Liu et al., 2025) or intensified chemical weathering (Liu et al., 2024a) under CO_2-induced "hothouse" conditions (Cao et al., 2022). These hypotheses all invoke enhanced deoxygenation and nutrient loading, but they differ fundamentally in the external source of nutrients and in the biogeochemical pathways by which ecological stress developed and persisted. Such uncertainty remains a key obstacle to a process-based understanding of why lacustrine ecosystems failed to regain stability during the Middle Triassic.

In this study, we present a high-resolution geochronological, mineralogical and geochemical dataset, including redox (iron speciation and redox-sensitive trace element systematics), and biogeochemical (C-N-S isotopes) and volcanic proxies, focusing on the YC7 interval in a continuous 400-m-long drillcore (Yao1) from a mid-depth lacustrine setting in the Ordos Basin, North China. We then integrate these results with biogeochemical modeling and a basin-scale compilation of C-S-P-Mo-U data from 24 drillcores to build a spatiotemporal visualization of the lacustrine redox structure and nutrient dynamics across the Mid-Triassic Ordos Basin. By investigating this earliest, iconic Mesozoic lacustrine record, we aim to clarify how external forcings and internal biogeochemical feedbacks instigated freshwater ecological

collapse and delayed recovery, with broader relevance to modern lacustrine ecocrises driven by anthropogenic emissions.

2. Geological setting

The Ordos Basin originates from the collision and assembly of the North China Block and Siberian Block, during which the rapid rise of the basin margin orogenic belt provided detrital sediment to the lacustrine setting (Yang et al., 2010; Yao et al., 2022; Zhao et al., 2020) (Fig. 1). The Yanchang Formation, from top to bottom, is divided into 10 members (YC1–YC10) based on marker beds, sedimentary cycles and lithological associations (Yang et al., 2010). The YC7 member contains high total organic carbon (TOC) concentrations, comprising mostly kerogen of type I or II (Fu et al., 2020; Zhao et al., 2018) (Figs. 1c and S1), marking one of the most important Mesozoic petroleum systems. The dating and stratigraphic correlation of the Yanchang Formation have long been subject to considerable debate (Bian et al., 2025). This uncertainty stems from the inherent variability of continental sedimentary sequences and the scarcity of index fossils. Both dating methods that have been applied to the succession (CA-ID-TIMS and LA-ICP-MS), indicate that YC7 deposition began at ~241 Ma (see below), consistent with Asseretospora-Apiculatisporites-Chordasporites palynological assemblages of Middle–Late Triassic age (Jin et al., 2021; Zhao et al., 2020). In this study, we rely on new U-Pb geochronology, which coincident with previous dating work (see Supplementary Material for further information on the geological background).

3. Methods

3.1. Sampling

Samples were collected from the 400-m-thick Yao1 drillcore located in the southeast Ordos Basin (Fig. 1). The selected samples were subjected to detailed sedimentology and geochemistry, comprising TOC (n = 276), XRD of total rocks (n = 284) and clay minerals (n = 284), iron speciation (n = 93), major and trace element measurements (n = 93), total nitrogen (TN) and N isotopes ($\delta^{15}N_{total}$) (n = 93), Hg concentrations (n = 93), organic carbon isotopes ($\delta^{13}C_{org}$) (n = 93), and pyrite sulfur isotopes ($\delta^{34}S_{py}$) (n = 93). Two ash-bed samples from near

the base and upper part of the main black-shale interval were analyzed for U-Pb dating, thereby bracketing most of YC7 black-shale deposition. In our attempt to be brief, here we only provide the key details of the analytical methods, while the full descriptions of experimental analyses and modelling approaches are given in the Supplementary material.

3.2. U-Pb dating

Samples Yao1-T1 and Yao1-T2 were collected for LA-MC-ICP-MS U-Pb dating via a Resonetics RESOlution M-50-HR excimer laser ablation system. Zircons from sample Yao1-T1, at the base of the organic-rich shale of YC7, gave an age of 241.36 ± 0.12 Ma (2s). The second sample, Yao1-T2, from the middle of YC7, yielded an age of 240.72± 0.07 Ma (2s). Integrating with previous age data, the lower and upper age limits of the YC7 organic-rich shale are ~241.36 Ma and ~240.0 Ma, respectively.

3.3. TOC and TN analysis

TOC and TN were measured using an Elementar Vario EL cube EA with decarbonated samples. Quality control checks were performed after every 10 samples, including sample duplicates, analysis of certified reference materials (acetanilide), and analysis of blanks. The measurement precision was better than ±0.1 wt% for TOC and ±0.3 wt% for TN.

3.4. Major and trace elements

Major and trace element concentrations were determined using a PANalytical Zetium X-ray fluorescence spectrometer and an Agilent 7500a inductively coupled plasma mass spectrometer (ICP-MS), respectively. For major element analysis, powdered samples were fused into glass beads and measured via wavelength-dispersive XRF. Trace element quantification involved acid digestion of sample powders with a mixture of HNO_3 and HF prior to ICP-MS measurement. Analytical precision, assessed through repeated measurements of certified reference materials (GBW07132, GBW07133, and GBW07407 for major elements; AGV-2, BHVO-2, BCR-2, and GSR-1 for trace elements), yielded relative standard deviations better than 5% for major elements and below 2% for trace elements.

The CIA parameter was calculated from the ratio of Al to major base oxides (Algeo et al., 2025; Nesbitt and Young, 1982):

$$CIA = Al_2O_3 / (Al_2O_3 + K_2O + Na_2O + CaO^*) \times 100 \quad (1)$$

where all variables represent the molar amounts of major-element oxides. CaO* represents the fraction of CaO in silicate minerals, which is used in place of total CaO in order to avoid contributions of CaO from carbonate and phosphate minerals that are not tightly linked to weathering processes. Enrichment factors (EFs) for trace elements were calculated as:

$$X_{EF} = (X/Al)_{sample} / (X/Al)_{AUCC} \quad (2)$$

where X is the element of interest (i.e., Mo and U), and AUCC represents the average upper continental crust (McLennan et al., 2001).

3.5. Iron speciation

The iron (Fe_{py}) and sulfur (S_{py}) contents in pyrite were determined stoichiometrically based on the weight percentage of Ag_2S obtained via chromium reduction analyses (Canfield et al, 1986). For iron associated with carbonate, magnetite and (oxyhydr)oxides, a sequential extraction procedure (Poulton and Canfield, 2005) was applied to approximately 0.1 g of powdered sample. The extraction sequence began with sodium acetate treatment at 50°C (pH 4.5, 48 h) to isolate carbonate-bound iron (Fe_{carb}). The remaining solid was subsequently exposed to sodium dithionite at room temperature (pH 4.8, 2 h) to dissolve (oxyhydr)oxide phases (Fe_{ox}). Finally, magnetite (Fe_{mag}) was extracted using ammonium oxalate (room temperature, 6 h). Iron concentrations in all extracts were quantified via inductively coupled plasma optical emission spectrometry (ICP-OES, Agilent 710), achieving an analytical precision better than 5% for all stages. The sum of Fe_{carb}, Fe_{ox}, Fe_{mag} and Fe_{py} gives a highly reactive Fe pool (Fe_{HR}) that is considered highly reactive towards dissolved sulfide in the water column and during diagenesis (Raiswell and Canfield, 1998; Poulton et al., 2004).

Boundaries for distinguishing anoxic water column redox conditions based on Fe speciation have been calibrated in a wide variety of modern and ancient marine settings (e.g., Raiswell and Canfield, 1998; Poulton and Canfield, 2011; Poulton, 2021). These calibrations suggest that Fe_{HR}/Fe_T ratios (where Fe_T represents total Fe) above 0.38 indicate deposition from anoxic bottom waters, while Fe_{py}/Fe_{HR} ratios above 0.6–0.8 are generally diagnostic of a euxinic water column (Poulton and Canfield, 2011; Poulton, 2021). Low Fe_{py}/Fe_{HR} ratios (<0.6) suggest that when anoxic, the water column was ferruginous rather than euxinic (Poulton, 2021). Although care is required when applying marine sediment iron speciation thresholds to

lacustrine sediments, this approach has been successfully applied to larger lacustrine settings (Cumming et al., 2013; Liu et al., 2024b), where the Fe shuttle that leads to Fe_{HR} enrichments under anoxic water conditions (Raiswell and Canfield, 1998; Severmann et al., 2008) may still operate. Indeed, the consistent interpretations between our Fe speciation and independent redox-sensitive trace metal data (see below) support a robust redox interpretation.

3.6. Pyrite-S $\delta^{34}S$ analysis

Pyrite-S isotope ($\delta^{34}S_{py}$) analyses were performed on Ag_2S precipitates from the chromous chloride extractions using an Elementar PYRO cube coupled to an IsoPrime continuous flow mass spectrometer. Laboratory standard SWS-3A ($BaSO_4$, $\delta^{34}S$ = +20.3‰), inter-laboratory standard CP-1 (chalcopyrite, $\delta^{34}S$ = −4.56‰), and international reference standard IAEA S-3 ($\delta^{34}S$ = −32.06‰) were used to check precision and accuracy. Replicate analyses yielded an accuracy of <0.33‰, and a precision of <0.3‰ (1 σ) for $\delta^{34}S$.

4. Results

Our zircon U-Pb dating from two ash beds that bracket the YC7 member gave ages of 241.36 ± 0.12 Ma (n=4) and 240.72±0.07 Ma (n=4) (Figs. 2 and S2). These data are consistent with previous results and confirm that the Ordos Basin represents the earliest known deep perennial lake system developed after the EPME (Jin et al., 2021; Zhao et al., 2020). Scanning electron microscope (SEM) images from the middle of the organic-rich shale unit in YC7 reveal abundant chrysophyte fossils and a large proportion of pyrite framboids and clusters (Figs. 2a and S3). These chrysophyte fossils exhibit various surface ornamentations and body sizes, belonging to the classes Chrysophyceae and Synurophyceae (Zhang et al., 2016). This unit also contains abundant lenticular carbonate fluorapatite (CFA) nodules (ranging from hundreds of micrometers to millimeters in length) (Zhang et al., 2021).

Total organic C and S_{py} exhibit increases from low levels in YC8 (TOC <2 wt%; S_{py} <0.5 wt%) to peaks in lower YC7 (TOC >25 wt%; S_{py} >5 wt%), followed by a return to low levels in upper YC7 to YC6 (Fig. 2c). Based on the redox reconstructions detailed below, the study interval can be divided into four stages [Stages I (300–250 m), II (250–235 m), III (235–220 m) and IV (220–158 m)], which coincide with oxic, ferruginous, euxinic and ferruginous water

redox conditions, respectively (Fig. 2d-e). Highly reactive iron over total iron ratios are low in Stage I, indicating oxic depositional conditions, and rise to values that are persistently above 0.38 (the lower boundary for identification of anoxia; Poulton and Canfield, 2011) from Stage II onwards. Pyrite iron over highly reactive iron ratios rise to values >0.6 in Stage III, documenting a transition from ferruginous conditions in Stage II to euxinic conditions in Stage III (Poulton, 2021). This is followed by a drop to lower Fe_{py}/Fe_{HR} values in Stage IV, with persistently elevated Fe_{HR}/Fe_T ratios suggesting a return to anoxic ferruginous conditions (Fig. 2d). These redox dynamics are supported by molybdenum and uranium enrichment factors (Mo_{EF} and U_{EF}), with peaks in U_{EF} that begin to form under anoxic, ferruginous conditions in Stage II, followed by highly elevated Mo_{EF} (>100) and U_{EF} (>20) values in Stage III (Fig. 2e), consistent with water column euxinia (Tribovillard et al., 2006). Moderately elevated U_{EF} and Mo_{EF} values in Stage IV, relative to oxic values in Stage I, also support a return to ferruginous conditions across this interval (Fig. S4).

Organic C isotopes show an initial steady state at ca. –27‰ in Stage I to early Stage II, followed by a decrease to <–30‰ in mid-Stage II to early Stage IV, and then a rebound to –27‰ to –29‰ in mid-Stage IV (Fig. 2f). Total nitrogen isotopes exhibit large fluctuations throughout Stages I to IV, with several samples having $\delta^{15}N_{tot}$ values < +1.5‰ in Stage III (Fig. 2f). Molar TOC/P increases to values higher than the classical Redfield C:P ratio of 106:1 from mid-Stage II to lower Stage IV (Fig. 2g), corresponding to the perturbations in TOC, redox data and $\delta^{13}C_{org}$. Molar TOC/N ratios also show a pulsed increase from <~6.6 (i.e., the Redfield ratio of 106:16) to >15, coincident with the increase in TOC/P (Fig. 2g). P/Al ratios (in ppm/%) rise from <87 (the average upper continental crust value) to >200 in Stage III (Fig. 2h). Pyrite S isotope values document a significant decrease, from as high as +5‰ to <–20‰ through Stage II (Fig. 2h), with minimum values coincident with the start of increasing TOC, S_{py}, Fe_{HR}/Fe_T and TOC/P values.

Clay mineral analysis shows that kaolinite over the sum of kaolinite and illite [Kao/(Kao+Ill)] ratios exhibit a rapid, short-term positive shift to >0.8 in Stage II, followed by a decrease to a very low level in Stage III, and then a rebound to ca. 0.2 thereafter (Fig. 2h). Hg/TOC (ppm/%) ratios are generally low (~10-30) with a marked decrease in Stage III (Fig.

2j), while the chemical index of alteration (CIA) is characterized by fluctuations between ~70 and ~40 through Stage II to IV (Fig. 2i).

5. Discussion

5.1. Lacustrine eutrophication and the collapse of ecological diversity

Our multi-proxy dataset suggests that extreme eutrophication, associated with algal proliferation and euxinia, impeded ecological stability in the YC7 Ordos Basin. Hyper-enrichment in TOC (>25 wt%) and S_{py} (>5 wt%) indicates elevated organic-matter accumulation and active microbial sulfate reduction (MSR; $SO_4^{2-}+2CH_2O \rightarrow 2HCO_3^{2-}+H_2S$) during Stage III, which is supported by the association of planktonic algal fossils and pyrite framboids in this layer (Figs. 2a and S3). These signals likely reflect both enhanced productivity and improved preservation of organic matter under reducing conditions. Redox proxies (iron speciation and Mo_{EF}-U_{EF}) track a transition from the development of ferruginous conditions in Stage II to euxinia in Stage III (Fig. 2d-e). The co-occurrence of algal proliferation and euxinia likely reflects a positive feedback among organic-matter production, oxygen depletion, and enhanced nutrient availability.

We infer that such a "domino effect" pushed the lacustrine ecosystem beyond its resistance threshold (Path 1 in Fig. 2b), leading to the collapse of hydrophyte-dominated trophic structures and the establishment of algae-dominated trophic structures (Tipping Point 1; Fig. 2b and 2f) (Dakos et al., 2019). The negative shift in $\delta^{13}C_{org}$ from >–27‰ to <–30‰ in Stage II provides prima facie evidence for this ecological succession (Fig. 2f), as planktonic algae typically exhibit lower $\delta^{13}C_{org}$ values than hydrophyte due to the distinct photosynthetic fractionation mechanisms and carbon fixation pathways. This ecological succession has been verified further by a combined molecular and biomarker assessment. Higher pristane/phytane (Pr/Ph) ratios and lower C_{24}/C_{26} tetracyclic terpane (C_{24}/C_{26} TT) ratios in YC8 have previously been interpreted to represent more oxidizing conditions and/or greater terrestrial-plants inputs (Bian et al., 2025; Zhang et al., 2021). Current biomarker evidence does not uniquely distinguish terrestrial plants from hydrophyte in the pre-YC7 interval, and we conservatively interpret the background system as mixed, while tentatively favoring a stronger contribution from aquatic macrophytes

based on the absence of charcoal record (Zhang et al., 2021). This preference arises from lower Pr/Ph and higher C_{24}/C_{26} TT ratios in YC7, indicating more reducing conditions and a greater algal contribution (Bian et al., 2025; Zhang et al., 2021). A high proportion of low-molecular-weight *n*-alkanes in YC7 further supports a strong contribution from aquatic algae and heterotrophic bacteria to the sedimentary organic matter (Xu et al., 2023).

Stage III samples with $\delta^{15}N_{tot}$ <1‰ (Fig. 2f) suggest that the expansion of ammonium-rich oxygen-deficient zones stimulated nitrogen fixation by algae/cyanobacteria (i.e., diazotrophs). These observations indicate that aquatic algae and heterotrophic bacteria proliferated in the YC7 Ordos Basin, providing a persistent ecological stressor, significantly impeding the reorganization of trophic networks on geological timescales (Mays et al., 2021). In turn, external stress unloading would have triggered the reverse feedback loop (Path 2 in Fig. 2b), reducing algal growth and anoxia sufficiently for macrophyte re-establishment, resulting in a recovery to better oxygenated water column conditions after the algal lacustrine ecosystem was pushed beyond its resilience threshold (Tipping Point 2; Fig. 2b), as supported by redox proxies and $\delta^{13}C_{org}$-$\delta^{15}N_{tot}$ data for Stage IV. We therefore interpret the YC7 interval as recording a pronounced ecological state shift from possibly aquatic macrophyte-rich to algae-dominated conditions, followed by delayed recovery (Dakos et al., 2019) (Fig. 2b), which has important ramifications for exploring the mechanisms of biogeochemical perturbations in both modern systems and the geologic record.

5.2. Sulfate as a cryptic driver of protracted lacustrine eutrophication

In many modern systems, lacustrine eutrophication and the expansion of marine 'dead zones' has occurred due to enhanced input of nutrients—typically in the form of nitrogen and phosphorus from fertilizers (e.g., Rabotyagov et al., 2014). In this study, however, based on an integrated multiproxy analysis, we propose that the protracted eutrophication that occurred in the Ordos Basin through the YC7 interval, leading to hydrogen sulfide poisoning and changes in trophic structure, was sustained primarily by endogenous P recycling triggered by a transient increase in external sulfate input.

Nutrient geochemistry demonstrates a significant increase in P availability via endogenous

P recycling. Molar TOC/P ratios increase from <30 in Stage I to higher than the classical Redfield ratio of 106:1 in Stages II and III (Fig. 2g), in parallel with the rise in TOC (Fig. 2c) and P/Al (Fig. 2i), the development of euxinia (Fig. 2d), and perturbations in C-N isotopes (Fig. 2f). Although Redfield stoichiometry was derived from marine plankton, a global synthesis of freshwater and marine settings indicates a broader mean ratio of C:N:P=166:20:1 (Sterner et al., 2008). Even relative to this broader benchmark, several samples show exceptionally high molar TOC/P ratios (up to >400; note that our ratios include detrital P in the total P pool, and so represent minimum values relative to initial organic C/P ratios), higher than the common TOC/P ratio of ~50–300 observed in anoxic environments (Algeo and Ingall, 2007) (Fig. 2g), and the only known process capable of rapidly generating such a high TOC/P ratio is via preferential release of P during anaerobic organic-matter remineralization (e.g., Ingall and Jahnke, 1994). Furthermore, the increase in molar TOC/N (>16) in Stage III also suggests nitrogen recycling alongside P recycling (Fig. 2g).

Sulfur isotope and clay mineral data suggest that P mobilization was mainly driven by degradation of organic matter on the lakebed induced by external sulfate supply. $\delta^{34}S_{py}$ values show a significant drop to <–20‰ in Stage II (Fig. 2h), with minimum values coincident with the first rise in both Fe_{HR}/Fe_T (Fig. 2d) and TOC/P (Fig. 2g). The present-day sulfate concentration in freshwater lakes is generally less than 800 μM, which is considered insufficient to fuel extensive microbial sulfate reduction (Hansel et al., 2015). The MSR-induced S-isotopic fractionation (ε_{MSR}) is consequently limited by a lower rate of MSR, which gives a higher $\delta^{34}S_{py}$ with smaller ε_{MSR} (Algeo et al., 2015; Gomes and Hurtgen, 2015). Therefore, the observed decline in $\delta^{34}S_{py}$ in Stage II can be plausibly explained by an increase in sulfate availability in the Ordos Basin. For the rebound in $\delta^{34}S_{py}$ across Stage III and the remainder of the section, the excess abundance of organic matter (TOC >25 wt%) would have increased the rate of MSR and thus decreased ε_{MSR} between residual sulfate and fixed pyrite in the sediments.

Further evidence comes from Kao/(Kao+Ill) ratios, which show a rapid, short-term positive shift in Stage II (Fig. 2h), suggesting a distinct kaolinitization event in parallel with the drop in $\delta^{34}S_{py}$. The most likely explanation for this coupling is the precipitation of acid rain and fast buffering, because kaolinite, as a mature weathering product, is much more stable under

316 acidic conditions relative to illite (Dill, 2016; Frings, 2019). Together, the coupled shift in $\delta^{34}S_{py}$
317 and Kao/(Kao+Ill) suggest a short-lived increase in external sulfate availability during Stage II.
318 Given that the kaolinite excursion is consistent with transient acidification, this perturbation is
319 most plausibly linked to volcanogenic sulfur delivery and associated acid precipitation,
320 although a subsidiary contribution from catchment weathering and evaporite dissolution cannot
321 be completely excluded (see discussion below).

322 A transient increase in external sulfate supply, together with mobilized P, initially
323 promoted ferruginous anoxia through enhanced productivity, followed by the development of
324 eutrophication and euxinia (Fig. 3a). In Stage II, the sulfate and P perturbation first promoted a
325 ferruginous benthic state (Fig. 2d) and stimulated P mobilization during early diagenesis in
326 porewaters (Fig. 3a). Rates of sulfate reduction then accelerated, pushing the system towards
327 euxinia in Stage III, during which organic phosphorus (P_{org}) and phosphorus associated with Fe
328 (oxyhydr)oxide minerals (Fe-P) were extensively recycled. Surplus H_2S that escaped burial
329 and diffused into the surface water could then be reoxidized to sulfate by reaction with dissolved
330 oxygen ($H_2S+2O_2 \rightarrow SO_4^{2-}+2H^+$). This newly generated sulfate would have further fueled MSR
331 in the water column and pore waters (Jørgensen and Kasten, 2006), leading to cyclic utilization
332 of sulfate (Fig. 3a) and thereby extending the aqueous residence times of sulfate and P. This
333 recycling process would have operated until sulfate was depleted via pyrite burial to a
334 concentration whereby rates of sulfate-controlled MSR were too low to challenge the critical
335 threshold of lacustrine ecological resilience (i.e., Tipping Point 2; Figs. 2b and 2f). The recycled
336 P_{org} and Fe-P increased the supersaturation of HPO_4^{2-}/PO_4^{3-} ions in porewaters, ultimately
337 precipitating in sediments as CFA, as suggested by the abundance of lenticular phosphate
338 nodules in this unit (Yuan et al., 2017; Zhang et al., 2021). Therefore, euxinia and eutrophic
339 conditions were able to persist for a prolonged period through Stage III (Fig. 2d-e) after the
340 cessation of the initial external forcing.

341

342 *5.3. Sources of sulfate and eutrophication*

343 By analogy with modern sulfidic lacustrine systems, sulfate can arise from three broad
344 source types: volcanogenic sulfur species (e.g., Lake Kivu, East African Rift; Tuttle et al., 1990),

evaporites dissolution via catchment runoff (e.g., Lake Cadagno, Switzerland; Berg et al., 2022), and seawater ingress into coastal lakes (e.g., Lake Suigetsu, Japan; Masuzawa and Kitano, 1982). Although the precise source of the initial sulfate pulse into the YC7 Ordos Basin cannot be demonstrated uniquely, the available evidence favors volcanogenic sulfur delivery as the primary driver of the Stage-II sulfate perturbation. Numerous ash beds and tuff interlayers within the Yanchang Formation indicate recurrent regional volcanism (Liu et al., 2025), and volcanogenic sulfur gases (e.g., SO_2, H_2S) released during ash-producing eruptions would have been oxidized to sulfate aerosols and sulfuric acid, delivering sulfate to the basin via atmospheric fallout. We therefore do not infer that sulfate entered the lake solely by direct atmospheric fallout. The transient kaolinite enrichment (Kao/(Kao+Ill) > 0.8) in Stage II is also consistent with such acidification, which suggests acidification-enhanced weathering within the catchment, and implies that part of the sulfate, together with some dissolved phosphorus and trace metals (e.g., Mo, U), may have been transferred to the lake through riverine and groundwater pathways. In this sense, volcanogenic sulfur oxidation is interpreted here as the principal ultimate source of the sulfate perturbation, whereas catchment-mediated transfer likely influenced how that sulfur was spatially distributed within the basin.

This interpretation also helps explain why volcanism is inferred to have acted mainly as a short-lived trigger rather than as the direct long-term maintainer of euxinia in Stage III. Hg/TOC and Hg/S_{py} decrease through Stage III (Fig. 2j), and a similar phenomenon is observed for other volcanogenic heavy metals such as Cu and Cd (Fig. S1), arguing against sustained direct volcanic fertilization during euxinia. Instead, once ferruginous anoxia had developed in Stage II, sulfate-enhanced remineralization and internal phosphorus recycling would have intensified microbial sulfate reduction and promoted the later expansion of euxinia. By contrast, we consider evaporite dissolution to only be a secondary and presently unconstrained possibility, although evaporite was widely deposited around the Tethys Ocean in response to climate aridification during the Late Permian and Middle Triassic (Zhu et al., 2020; Li et al., 2014), as it does not readily account for the coeval acidity signal. We also exclude the possibility of seawater incursions as a source of sulfate in view of the low salinity Sr/Ca ratios (mean = 0.36, n = 93) that occur (Fig. S1), consistent with freshwater deposition, alongside an absence of

unequivocal marine fossils in the YC7 interval (Yao et al., 2022; Zhao et al., 2020).

Pearson's correlation coefficients between TOC and environmental variables reveal most significant positive relationships between TOC and TOC/P ($r = 0.89$, $p < 0.001$), and TOC and P/Al ($r = 0.82$, $p < 0.001$) (Fig. 3b-c). TOC also shows moderately strong positive correlations with both Fe_{py}/Fe_{HR} and S_{py} ($r = 0.77$, $p < 0.001$), which may indicate either that more sulfidic conditions favored OC preservation or, conversely, that enhanced OC production fuels MSR and thereby promotes euxinia. The absence of significant positive correlations with other parameters (e.g., Hg/TOC, Cu/TOC, Cd/TOC and CIA) supports the suggestion that the high productivity and eutrophication was sustained by endogenous P recycling under euxinic conditions, further highlighting the importance of sulfate as a manipulator of the collapse of lacustrine ecological diversity.

5.4. Modelling a transient external sulfate influx

As a consequence of the existence of hysteresis, the changing of biological and geochemical states usually lags behind the external force loading or unloading. The strength of this hysteresis determines ecosystem resilience, with stronger hysteresis making state reversal more challenging. Notably, the present dataset documents one transition into the stressed state and one transition out of it, rather than repeated oscillation between two formally defined stable states. The analogy to modern alternative-state theory is therefore conceptual rather than exact, and is used only to highlight lagged ecological recovery relative to the external forcing.

We therefore explore the lacustrine C-O_2-P-S-N biogeochemical cycles in the YC7 Ordos basin based on a scaling-down of the global processes in the COPSE (Carbon Oxygen Phosphorus Sulfur Evolution) model (Lenton et al., 2018; Fig. S5), and further consider the background atmospheric composition post-EPME, along with MSR, H_2S reoxidation, sulfate-driven P recycling, and the dependence of ε_{MSR} on $[SO_4^{2-}]$. Our model treats the lacustrine water-sediment system as a single reservoir that is well-mixed and homogeneous on a million year timescale, and depends only on influxes and outfluxes, without regard for density stratification. Within this framework, we reasonably shrink oceanic reservoirs (e.g., carbon, sulfur and phosphorus) and fluxes (weathering, degassing and burial) by seven orders of

magnitude to match the size of the Ordos Basin, while keeping atmospheric oxygen and carbon dioxide levels at a 'Triassic-like' steady state (i.e., pO_2 = 1 PAL and pCO_2 = 1 PAL, where PAL = present atmospheric level) during the model runs. See Tables S1–S4 for a full model description.

Our modified COPSE model reproduces the first-order temporal relationships observed in the dataset, especially prolonged euxinia (given as 'Anox' >0.9) and increased P recycling over time (Fig. 4). Figure 4a shows a negative excursion in modelled $\delta^{34}S_{py}$ forced by the external sulfate input, among which the best fit with $f_{pysb} \approx 0.5$ gives a nadir of ca. –20‰, followed by a rapid rebound to ca. +5‰ (dotted lines in Fig. 4a), generally replicating the observed $\delta^{34}S_{py}$ record (Fig. 2h). Figure 4b shows that 'Anox' monotonously increases alongside the onset of the sulfate input and recycled P, reaching its peak after the unloading of the pulse. This finding is consistent with the observed temporal hysteresis of peak euxinia in Stage III (Fig. 2d-e) versus the $\delta^{34}S_{py}$ anomaly (Fig. 2g). Moreover, the modeled duration of anoxia is far longer than the external forcing, while the former is dependent on f_{pysb}, such that a smaller f_{pysb} yields a longer timespan of peak 'Anox'. A value of f_{pysb} = 1 gives the peak 'Anox' (> 0.9) for ca. 0.7 Myr (lower limit), f_{pysb} = 0.5 prolongs it to ca. 0.85 Myr (green full line), and f_{pysb} = 0.1 prolongs it to ca. 1.1 Myr (upper limit). These findings reflect that a given lower rate of pyrite burial means more H_2S diffusing upwards to be reoxidized to sulfate, which fuels further MSR (Fig. 3a) and thus prolongs the residence times of sulfate and P in the lacustrine ecosystem (Fig. 2b).

The modelled $C_{org}/P_{reactive}$ ratios (where $P_{reactive}$ is the sum of P_{org}, Fe-P and authigenic P; Fig. 4e) show an increase from <60 to >240, indicating a moderate degree of P recycling, consistent with the TOC/P data (Fig. 2g). The modelled burial rates of P_{org} (OPB; Fig. 4c) and Fe-P (FePB; Fig. 4d) show a secular decrease alongside the peak in 'Anox', which supports our hypothesis that P recycling was driven by organic remineralization and release of P during sulfide-promoted abiotic reduction of Fe (oxyhydr)oxides (Poulton et al., 2004). Recycled P can be returned by mixing and diffusion back to the surface to fuel renewed primary productivity, thus supporting further burial of organic carbon (OCB) and pyrite (PYB) (Fig. 4f). Enhanced organic carbon burial (OCB) is slightly more prolonged than pyrite burial (PYB) in the model because internally recycled P can continue to sustain productivity after sulfide burial

begins to wane.

Our model results thus show a strong level of qualitative and quantitative agreement with independent geochemical proxies and their behavior over time, despite the fact that the model only focuses on temporal offsets and relative trends, rather than absolute values. We therefore propose that a transient external injection of sulfate and accompanying P drove strong endogenous P recycling, which in turn caused widespread eutrophication and hydrogen sulfide poisoning, enabling the lacustrine ecosystem to exceed its resilience, thereby resulting in a lengthy crisis for lacustrine biodiversity in the mid-Triassic Ordos Basin.

5.5. Spatial reconstruction of redox variability across the Ordos Basin

We mapped the spatial redox distribution across the YC7 Ordos Basin using a simplified one-dimensional, depth-dependent geochemical model, which is driven by ~1,100 C-S geochemical data points collected from the 18 studied cores/sections, representing the organic-rich shales of YC7 (for locations see Fig. 1). The model is intended to only explore first-order relative spatial contrasts in dissolved oxygen ([O_2]) and H_2S ([H_2S]), rather than absolute dissolved-gas concentrations, under a relatively quiescent lacustrine condition. Considering basin-scale advection and explicit aerobic respiration are difficult to independently constrain in this relatively low-energy lake setting, these terms are therefore omitted. At a certain site in the water column, the modeled [O_2] and [H_2S] are sourced by downwards diffusion of atmospheric O_2 across the air-water interface and MSR-derived H_2S upwards diffusion, respectively, and are also constrained by reaction together during H_2S reoxidation. For simplicity, we assume: (i) constant effective diffusivities with depth, (ii) a relatively quiescent water column within the modelled timescale (Myr), such that large storms and strong upwelling are not resolved, (iii) background climatic factors including pO_2, pCO_2 and water temperature remain unchanged, and (iv) relative water depth at each site was approximated from the thickness of the black-shale interval and is used here only to recover first-order basin geometry and relative position between sites, rather than absolute paleobathymetry.

Gridded dip-line cross-sections drawn with our spatial model visualize a first-order pattern of depth-dependent oxygen deficiency with a metastable sulfidic zone developed at mid-depth

(Fig. 5a–f), broadly consistent with the redox reconstructions for both the Yao1 core (Fig. 2d–e; Site 12 in Fig. 5) and the whole Ordos Basin based on published redox data (Fig. 5g–h). In nature, where in the water column and how quickly MSR proceeds (F_{MSR}) depends on the [SO_4^{2-}] and OC concentrations (Canfield and Farquhar, 2009), and a euxinic water mass may then develop at the location where the product of [SO_4^{2-}] and OC concentrations reach a maximum. In our model, the highest calculated F_{MSR}, and thus the oxygen-deficient zone, occurred at mid-depth sites (Sites 3–6 and 12–16; Fig. 5a–c). In anoxic basins today, mildly sulfidic deep waters are separated from the atmosphere by an oxygenated surface layer, at the base of which is a sulfidic chemocline through which O_2 concentrations fall to zero (Kump et al., 2005), and as such, the Black Sea provides a useful analog (Arthur and Sageman, 1994). However, our spatial redox simulation shows that the modelled diffusive flux of H_2S from below would increase beyond twice the supply of O_2 from the atmosphere across the air-sea interface at mid-depths, given a lower f_{pysb} (e.g., $f_{pysb} \leq 0.5$; Fig. 5d–f). This would have led to a shallow chemocline that may even have allowed H_2S emission to the atmosphere. This hyper-sulfidic condition in the nearshore watermass also applies to the Late Devonian (Sahoo et al., 2023), end-Permian (i.e., EPME) (Schobben et al., 2015) and Cenomanian-Turonian (Damsté and Köster, 1998), during which the locus of euxinic expansion in the shallow habitable zone of the oceans contributed to the pattern and severity of mass extinctions.

We hypothesis that such a redox distribution pattern, in which a metastable sulfidic zone developed at mid-depths, is more closely analogous to the "euxinic wedge" proposed for Precambrian anoxic oceans (Poulton et al., 2010; Li et al., 2010), although previous studies comparing it to the metalimnetic oxygen minima (MOM) of modern stratified lakes (Bian et al., 2025). Our model does not resolve the exact circulation pathway of sulfate within the basin, but it suggests that the maintenance of this sulfidic zone was primarily controlled by the co-availability of [SO_4^{2-}] and OC, such that MSR was strongest at mid-depths where the modelled product of the two substrates reaches a maximum. The volcanogenically-derived sulfur may have been transferred through acidification-enhanced catchment weathering and subsequent riverine and groundwater delivery, thereby generating a first-order proximal-to-distal gradient in net sulfate availability. By contrast, deeper waters likely remained mainly ferruginous

because microbial sulfate reduction was weaker there, either owing to reduced OC supply under lower productivity and/or to progressive sulfate consumption during basinward transport and reduction. This interpretation is consistent with the persistence of more ferruginous to dysoxic conditions toward the basin center (Fig. 5g–h), as also suggested by previous studies (Yuan et al., 2021; Zhang et al., 2022) (Fig. S6d–e).

5.6. Implications for modern lacustrine ecological crises

As a deep-time example of persistent eutrophication sustained by internal nutrient feedbacks, the mid-Triassic Ordos Basin may provide transformative insight for contemporary lake restoration strategies. Global lakes have experienced accelerating deoxygenation and eutrophication over recent decades, posing serious crises to the freshwater resources and ecological habitats that terrestrial life, including humans, rely on. Satellite remote sensing reveals that harmful algal blooms have expanded by ca. 58% globally over four decades (Ho et al., 2019), and dissolved oxygen concentrations have declined persistently in >83% of lakes (Zhang et al., 2025; Jane et al., 2021). However, despite strategies to reduce nutrient inputs, lacustrine eutrophication and algal blooms persist with unexpected resilience. For example, in Lake Gundsømagle (Holland), cyanobacterial proliferation continues after a 70% reduction in phosphorus loading over past decades (Søndergaard et al., 2013), while Bangalore lakes (India) show only 12% functional recovery despite a 7-fold increased restoration investment (Ramachandra et al., 2021; Søndergaard et al., 2005). Although nutrient oversupply from land use practices such as fertilizer application can exacerbate deoxygenation, our data more directly highlight sulfur loading as a mechanism capable of amplifying internal phosphorus recycling and prolonging eutrophic conditions.

We infer that sulfate, although not itself a nutrient, may have acted as an indirect facilitator of eutrophication, harmful algal proliferation and water-column deoxygenation, in not only the mid-Triassic Ordos Basin but also in many modern lakes (e.g., Lake Taihu, China; Lake Loosdrecht, Holland) (Chen et al., 2016; Søndergaard et al., 2013). Our modified COPSE model suggests that sulfate-driven lacustrine deoxygenation would have lasted at least 7 times longer than the sulfate loading time (Fig. 4). The development of mid-depth euxinia likely exert a

prolonged stranglehold on biological communities by drastically constraining habitable zones. Specifically, sulfide toxins inhibit the diversification of secondary consumers, and nutrient pathways triggered taxonomic and functional homogenization of aquatic organism communities at local and regional scales. The proposed "euxinic wedge" at mid-depth (Fig. 5) would have compressed the habitable zone of nekton and fish, as well as limiting biological connectivity and energy transfer between shallow and deep waters, thereby impeding reestablishment and maintenance of a complex food web, causing lacustrine ecosystems to remain fragile and unstable. For the modern world, the most relevant analogue is anthropogenic sulfur loading associated with fossil-fuel combustion, industrial emissions, and sulfate-rich catchment inputs, while legacy internal loading may delay recovery even after management intervention (Dadi et al., 2023).

6. Conclusions

We combined a high-resolution geochronological, mineralogical and geochemical dataset with biogeochemical models to develop a spatiotemporal visualization for interpreting lacustrine paleoredox conditions and nutrient dynamics in one of the oldest known Mesozoic-type lacustrine ecosystems. Moving beyond conventional explanations centered on external nutrient fertilization, we reveal a more subtle and insidious culprit: external sulfate inputs that ignited a cycle of self-sustaining, internal phosphorus recycling, extreme eutrophication, and widespread hydrogen sulfide poisoning. Sulfate-driven endogenous P recycling and hence lacustrine euxinia reconcile various geochemical records, but also explain the hyper-enrichment of hydrocarbons, pyrite and redox-sensitive elements during YC7 deposition, and emphasizes that internal sulfur–phosphorus feedbacks can sustain ecological stress beyond the duration of the initial forcing. Finally, to accurately predict lacustrine environmental change in response to current and future anthropogenic emissions and land use changes, it is essential to improve our understanding of the biogeochemical feedbacks that regulate endogenous phosphorus recycling, and particularly the role of sulfate, which is a topic currently lacking consensus in Earth System models.

CRediT authorship contribution statement

W. Shi: Data collection and analysis, Investigation, Visualization, Methodology and Writing – review and editing. **C. Li**: Conceptualization, Supervision, Visualization and Writing – review and editing. **R. Zhu**: Supervision and Visualization. **B.J.W. Mills**: Supervision, Visualization, Methodology and Writing – review and editing. **J. Cui**: Data collection and Methodology. **C. Wang**: Supervision, Visualization, Methodology and Writing – review and editing. **T.J. Algeo**: Supervision, Visualization, Methodology and Writing – review and editing. **M. Li**: Methodology and Writing. **M. Hou**: Supervision, Visualization, Writing – review and editing. **S.W. Poulton**: Supervision, Visualization, Writing – review and editing.

Declaration of competing interests

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

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Appendix A. Supplementary material

Supplementary material related to this article can be found on line at

Data availability

The original data generated in this study are provided in the Supplementary Data Files 1, 2.

Code availability

The code and output data are available from the corresponding author on request.

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762

763 **Figure captions**

764 **Fig. 1. Location and geological setting of the study sections. a.** Reconstructed
765 Paleogeography of the late Middle Triassic at ~240 Ma, including the location of the Ordos
766 Basin, North China. **b.** Isopach map of the organic-rich shale of Member 7 of the Yangchang
767 Formation (YC7) in the Ordos Basin, North China (Yang et al, 2010), including relative
768 estimated water depths. Circles with number represent the 24 drillcores in this study, among
769 which No. 12 is the Yao1 drillcore. **c.** Stratigraphic column of the Yangchang Formation in Yao1,
770 containing the distinguishable 'hot shale' of YC7 with high total organic carbon (TOC) and
771 hydrogen index (HI) values. **d.** East-west-oriented dip-line cross-section (Z to Z') with the
772 relative position of the 24 drillcores, basing on well-to-seismic calibration and strata thickness
773 of the Ordos Basin. Data sources are given in Table S5.

774

775 **Fig. 2. Lithostratigraphy, geochronology and chemostratigraphy of the Yao1 drillcore,**
776 **Ordos Basin. a.** Scanning electronic microscopy (SEM) images showing the coexistence of
777 Chrysophyte fossils and pyrite framboids. Abbreviation: Alg, algae fossils; Py, pyrite framboids.
778 **b.** Tipping points mark discontinuous changes in the states of a normal ecosystem (modified
779 from Dakos et al., 2019). Alongside external force uploading, the initial relatively oxygenated
780 ecosystem follows the equilibrium line (Path 1) until conditions cross Tipping Point 1, at which
781 point the oxic water disappears and the ecosystem state drops abruptly to a sulfide-stressed
782 eutrophic state. In turn, reducing external force—but to a much lower level—leads to the
783 restoration of the oxygenatedecosystem configuration at the crossing of Tipping Point 2. The
784 difference between the forward and backward tipping points marks the hysteresis in the system.
785 **c.** Concentration of total organic carbon (TOC) and pyrite sulfur (S_{py}). **d.** Iron speciation data.
786 Dashed blue line on the Fe_{HR}/Fe_T plot represents the defined boundary for identifying oxic and
787 anoxic deposition. The dashed red line on the Fe_{py}/Fe_{HR} plot distinguishes euxinic from
788 ferruginous deposition (for samples clearly deposited from an anoxic water column). **e.**
789 Molybdenum (Mo_{EF}) and uranium (U_{EF}) enrichment factors. **f.** Organic carbon isotope ($\delta^{13}C_{org}$)
790 and bulk nitrogen isotope ($\delta^{15}N_{tot}$) values. **g.** Molar TOC/P and TOC/N ratios. **h.** Pyrite sulfur

isotope ($\delta^{34}S_{py}$) values, and kaolinite normalized to the sum of kaolinite and illite [Kao/(Kao+Ill)] ratios. **i**. P/Al and chemical index of alteration (CIA) values. **j.** Hg/TOC and Hg/S_{py} ratios.

Fig. 3. Biogeochemical processes related to the development of sulfate-driven eutrophication in the palaeolake (a), heat map showing the relationships among different geochemical variables (b), and data compilation analysis showing the correlation between TOC and TOC/P (c). In (**a**), benthic organic carbon ($[CH_2O]_x$) is oxidized by microbial sulfate reduction (MSR) using external sulfate, most plausibly sourced by volcanogenic sulfur delivery, during which organic phosphorus (P_{org}) is released during remineralization. Part of the produced H_2S stimulated iron reduction (IR) and pyrite formation, during which iron-bound phosphorus (Fe-P) is released, while residual H_2S in the water column may be re-oxidized to sulfate, thereby promoting cyclic sulfur utilization and phosphorus recycling and hence eutrophication. In (**b**), with all data coming from the Yao1 drillcore, TOC has a high correlation with TOC:P (0.89) and P/Al (0.82), a moderate correlation with euxinia (Fe_{py}/Fe_{HR} of 0.77, Mo_{EF} of 0.77, U_{EF} of 0.73 and S_{py} of 0.77), but no correlation with weathering (CIA) and volcanic (heavy metals) proxies. In (**c**), paired TOC and TOC/P data for the YC7 organic-enriched shale are collected from drillcores No. 1–18.

Fig. 4. COPSE biogeochemical model results for lacustrine redox and nutrient dynamics with a forced input (S:P = 53:1) and varying fractions of pyrite burial (f_{pysb}). a. Pyrite sulfur isotopes (given as $\delta^{34}S_{py}$). **b.** Degree of water column anoxia. A value of 1 on the Y-axis means completely anoxic, while 0 means completely oxic. **c.** Burial flux of organic P. **d.** Burial flux of iron-bound P. **e.** Calculated $C_{org}/P_{reactive}$, where $P_{reactive}$ is the sum of organic P, iron-bound P and authigenic P. **f.** Burial fluxes of organic carbon (OCB) and pyrite sulfur (PYB).

Fig. 5. Spatial visualization of dissolved oxygen (a–c) and H_2S (d–f) concentrations with varying fractions of pyrite burial (f_{pysb}), and box plots of enrichment factors of redox sensitive elements (i.e., Mo_{EF} and U_{EF}) (g–h) across an east-west-oriented dip-line in the Ordos Basin during deposition of YC7 organic-rich shale. A total of 1,100 C-S data points from drillcores No. 1–18 were used to estimate first-order spatial pattern in [O_2] (**a–c**) and [H_2S] (**d–f**) concentrations. A total of 606 Mo_{EF}–U_{EF} data points from drillcores No. 1–8, 12–13, and 17–24 (**g–h**) were used for verifiable comparison with the modelling results shown in **a–f**. No. 12 denotes the Yao1 drillcore. See Supplementary material for sample location and model details (Figs. S6; Table S5–S6).