

Land-cover not climate controls lake-atmosphere carbon exchange since the Last Glacial Maximum

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Key Points:

- Carbon dynamics over the last 26 kyr reflect catchment vegetation changes and hydrological delivery of terrestrial DOC.
- Land-cover change and precipitation variability may influence aquatic C balances more than regional warming.

Abstract

Lake metabolism and associated emissions of CO₂ in lakes are heavily subsidized by terrestrial carbon but the role of climate forcing remains unclear. The carbon stable isotope composition of zooplankton in a sediment core from a sub-tropical alpine lake in SW China tracked atmospheric CO₂ and $\delta^{18}\text{O}$ records of monsoonal strength (Dykoski et al., 2005; Wang et al., 2005) over the last ~26 kyr. The lake was CO₂-limited during the Last Glacial Maximum (LGM) when C₄ vegetation dominated the catchment. Zooplankton production and inferred-lake CO₂ (from *Bosmina* $\delta^{13}\text{C}$) increased from 10 ka with strengthening of the SW Asian monsoon and forest expansion. These results highlight the importance of land-cover and hydrology in controlling terrestrial organic matter inputs to lakes and aquatic carbon dynamics at 10²-10³ yr timescales.

Plain Language Summary

Carbon dynamics in a sub-tropical alpine lake over the last 26 kyr reflect catchment vegetation changes and hydrological delivery of terrestrial DOC, suggesting that land-cover change and precipitation variability may influence aquatic C balances more than regional warming.

1 Introduction

Rising temperatures, altered hydrological pathways, and changes in land cover are resulting in fundamental changes in terrestrial-aquatic biogeochemical linkages (Creed et al., 2018). The carbon used by lake secondary producers (i.e. zooplankton) is a mixture between that fixed by aquatic primary producers and that transferred from catchment vegetation and soils, mainly as dissolved organic matter. The balance between the two sources depends on a range of factors (Tanentzap et al., 2017). However, any alteration in the supply of terrestrial carbon - the messenger between terrestrial and lake ecosystems (Creed et al., 2018) - has potentially profound effects on the structure and function of lakes and the emission of greenhouse gases. Terrestrially-derived organic material (t-OM) supports secondary production in lakes (Pace et al., 2004) but its role remains contentious (Grey and Jones, 2001; Tanentzap et al., 2017). It has been argued that t-OM is especially important in sustaining zooplankton in lakes that have low primary production (Carpenter et al., 2005). The amount of t-OM imported from the catchment may be several orders of magnitude higher than the amount of autochthonous OC that is generated inside the lake with resultant net CO₂ emissions from lakes (Sobek et al., 2003). The terrestrial subsidy to aquatic food webs can also stabilize population dynamics and predator-prey interactions and influence carbon emissions by lakes (Schindler, 1997). The balance between these auto- and heterotrophic C sources (primary production and respiration) varies both seasonally and over longer timescales (del Giorgio and France, 1996). How these linkages will be altered with both changing climate (precipitation as well as temperature) and land-cover is, however, unclear.

Terrestrial contributions to zooplankton have been estimated primarily by using zooplankton carbon stable isotopes ($\delta^{13}\text{C}$) (Grey and Jones, 2001) which closely reflect their diet (Fry and Sherr, 1984). It has also been shown to provide a measure of the baseline pelagic $\delta^{13}\text{C}$ of a lake (Smyntek et al., 2012) and the possibility of reconstructing aquatic CO₂ over timescales much longer than those covered by monitoring (Perga et al., 2016). Although many studies to date suggest significant use of t-OM by zooplankton, how its use varies in response to climate change is unclear, if only because of the widespread human impact on land-cover (Ellis et al., 2013) which confound climate signals in contemporary studies (Creed et al., 2018; Tanentzap et al., 2017).

Precipitation influences terrestrial-aquatic linkages and t-OM supply rates (Tranvik et al., 2009) and disentangling the role of terrestrial C against a background of climate change is crucial for understanding their interaction in the future. To date, much of the evidence for the effects of t-OM inputs is derived from spatial surveys and experiments in the temperate-boreal zone (Grey and Jones, 2001; Tanentzap et al., 2017). Alternatively, palaeoecological methods can be used to understand interactions at one site prior to the onset of anthropogenic landscape change. Here we used a multi-proxy palaeolimnological approach and inferred in-lake CO₂ from $\delta^{13}\text{C}$ of *Bosmina* ($\delta^{13}\text{C}_{\text{BOS}}$) (Perga et al., 2016) to test the hypothesis that zooplankton production and CO₂ dynamics in a large, deep sub-tropical lake (Lugu Lake, SW China) reflect climate-driven terrestrial subsidies since the Last Glacial Maximum (LGM, ~26 kyr).

Bosmina is ubiquitous in lakes world-wide and adapts to a variable food supply, changing their diet according to availability and its exoskeletons are abundant in lake sediments. While its potential food sources can include heterotrophic bacteria, nanoflagellates and ciliates, *Bosmina* is

primarily an herbivore, consuming phytoplankton (an assumption of the use of $\delta^{13}\text{C}_{\text{BOS}}$ to infer lake-water CO_2 (See SI and Perga et al. (2016) for a discussion).

2 Materials and Methods

2.1 Zooplankton stable isotope analyses

To extract sufficient numbers of cladoceran subfossil, a total of 32 subsamples, from 0-164 cm, 164-288 cm, 288-418 cm, 418-554 cm, 554-770 cm and 770-830 cm, were taken from Lugu sediment core. They are clusters of three samples at different depths. Isotope analyses were performed only on *Bosmina* remains, as *Bosmina* remains were abundant enough (abundances >80%). Freeze-dried cladoceran samples were heated for 30 min in KOH 10% at 70 °C in order to dissolve the organic labile constituents. Samples were then rinsed with deionized water, transferred in a beaker with HCL 10% for 5 min to remove carbonates (Nevalainen et al., 2014). Samples were rinsed one more time. *Bosmina* remains (head shields and carapaces) were sieved with 32- μm filter and thoroughly rinsed. The remaining materials were *Bosmina* exoskeletons. Exoskeletons were then sorted under a dissecting microscope and packed into tin cups in order to reach 0.2 mg dry weight (Perga, 2010). Previous experiments performed on cladoceran subfossil remains have demonstrated that these chemical treatments and taphonomic processes have minor effects on the $\delta^{13}\text{C}$ values obtained for the remains (Perga, 2011). C stable isotope composition was measured from Deltaplus mass spectrometer (Thermo Fisher Scientific Inc., West Palm Beach, FL, USA). Their composition was expressed in the conventional δ notation, defined as per mil (‰) deviation against VPDB.

2.2 Calibration of the paleoproxy for $\text{CO}_{2\text{aq}}$

The seasonal data for cladoceran $\delta^{13}\text{C}$ values were available and dissolved CO_2 concentrations ($\text{CO}_{2\text{aq}}$) (as the sum of dissolved CO_2 and H_2CO_3) in the water column was calculated following Stumm and Morgan (1995), accounting for lake water pH, temperature, and DIC concentrations (Cole et al., 1994) using Visual MINTEQ version 3.1 (Gustaffson, 2013). A log linear regression model linking surface lake CO_2 concentrations and *Bosmina* $\delta^{13}\text{C}$ values was computed from the Lugu Lake seasonal monitoring data set and compared with a model previously developed for Windermere (Smyntek et al., 2012). As in Perga et al. (2016), we tested the ability of the model to predict past CO_2 concentrations using monitoring data. The CO_2 concentrations from the water columns over the last 26 kyr were reconstructed from subfossil cladoceran $\delta^{13}\text{C}$ values using the model established in Smyntek et al. (2012).

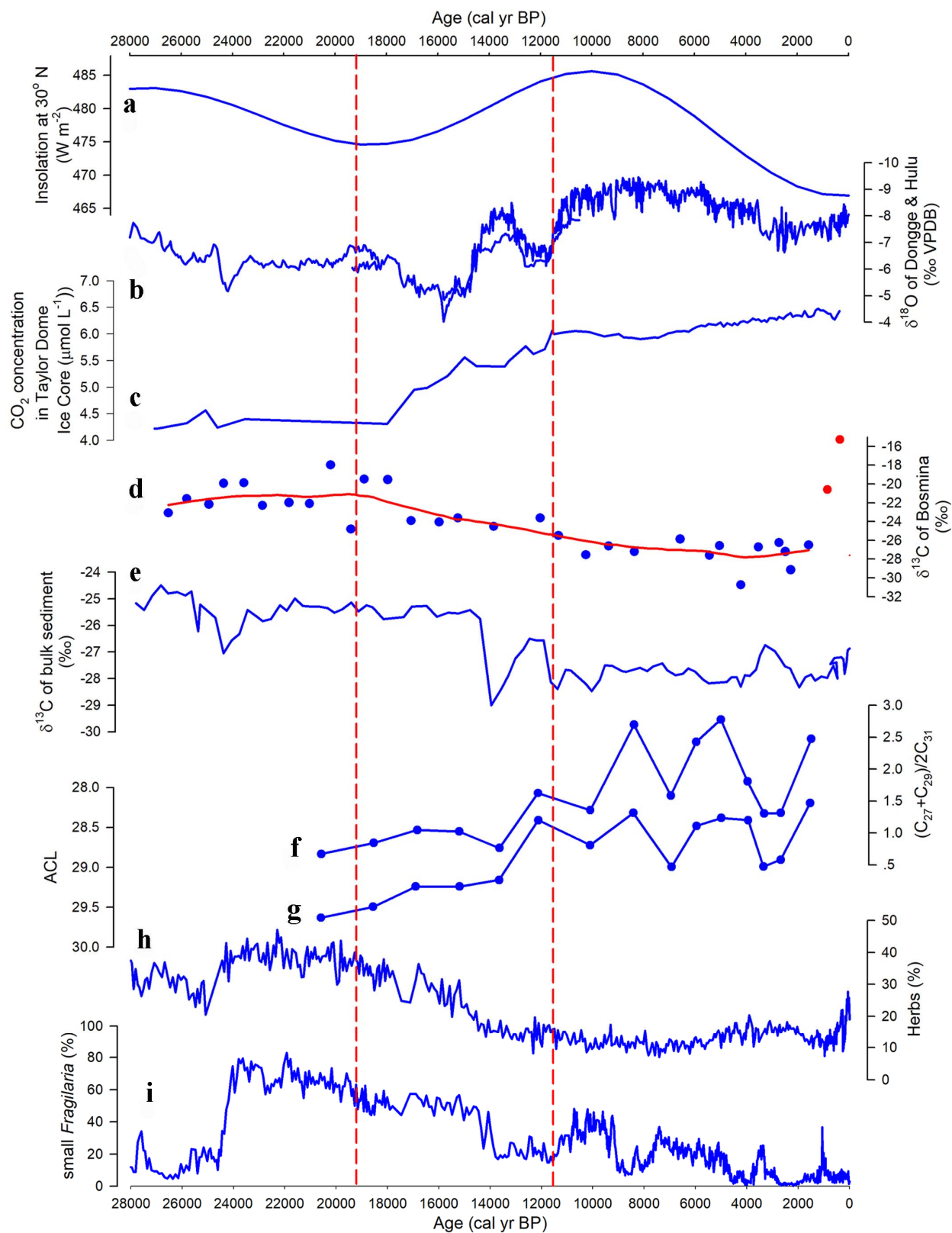


Fig. 1. Comparisons of the regional and local records around Lugu Lake during the last 28 ka. (a) Solar insolation (July) at 30° N (Berger and Loutre, 1991). (b) $\delta^{18}\text{O}$ data from Dongge and Hulu Cave (Dykoski et al., 2005; Wang et al., 2001). (c) CO_2 concentration from Taylor Dome Ice Core (Smith et al., 1999). (d) $\delta^{13}\text{C}$ of *Bosmina* from Lugu Lake. (e) $\delta^{13}\text{C}$ of bulk sediment from Lugu Lake. (f) *n*-alkanes parameters: $(\text{C}_{27}+\text{C}_{29})/2\text{C}_{31}$ and (g) average carbon length (ACL) from Lugu Lake. (h) Percentages of herbs from Lugu Lake. (i) Percentages of small benthic *Fragilaria* from Lugu Lake. The fitted curves are loess smoothers (span 0.3, red lines).

3 Results and Discussion

3.1 *Bosmina* dominance during 26 ka

With the exception of the period 22–19 ka (years before the present, where the “present” is defined as the year 1950 A.D.; see Supplementary Information), the zooplankton community at Lugu Lake was dominated by the pelagic cladoceran *Bosmina* [(*Eubosmina*) *coregoni*, *B. longispina*, and *B. longirostris*] for more than 20 kyr (Fig. S4). The total cladoceran accumulation rate (AR) was extremely low during the LGM but the abundance and AR of pelagic *Bosmina* taxa showed an abrupt increase after 18 ka and reached ~ 600 inds $\text{cm}^{-2} \text{yr}^{-1}$ around 11 ka (Fig. S4). The $\delta^{13}\text{C}$ of bulk sediment (OM_{sed}) ranged from -27.0‰ to -24.5‰ , and the C/N ratio and C sedimentation rate were low (8.8–11.1 and $0.3\text{--}2.9 \text{ g C m}^{-2} \text{yr}^{-1}$ respectively). In contrast, the $\delta^{13}\text{C}_{\text{BOS}}$ was enriched up to -18‰ and the greatest differences between OM_{sed} and *Bosmina* $\delta^{13}\text{C}$ occur at this time ($\sim 4\text{‰}$) (Fig. 1d and e).

3.2 Terrestrial input during the Last Glacial cycle

$\delta^{13}\text{C}_{\text{BOS}}$ tracks atmospheric CO_2 concentration recorded in the Taylor Dome ice core (Smith et al., 1999) ($r=0.72$, $P<0.0001$; Fig. 1b, c and Fig. 2c). A *Bosmina*- CO_2 inference model suggests that the lake was under-saturated with respect to atmospheric CO_2 ($1.0 \mu\text{mol L}^{-1}$ versus $4.7 \mu\text{mol L}^{-1}$). The climate around Lugu Lake during the LGM was dry and cold, perhaps $\sim 5\text{--}6^\circ\text{C}$ cooler than today. The increased aridity and low atmospheric CO_2 concentration drove an expansion of C_4 plants (e.g., *Artemisia*, *Cyperaceae*) during the LGM around Lugu Lake as observed elsewhere (Ehleringer et al., 1997; Street-Perrott et al., 1997). C_4 plants possess a CO_2 concentrating mechanism and have low levels of respiratory inhibition of photosynthesis (Farquhar et al., 1989), and so have an important advantage over C_3 plants at times of low atmospheric CO_2 partial pressure ($p\text{CO}_2$)/ O_2 ratios (Sage, 2001). The C_4 pathway characteristic of herbs leads to $\delta^{13}\text{C}$ values between -17‰ and -9‰ while C_3 plants range from -32‰ to -20‰ (Deines, 1980). The enhanced contribution of C_4 plant biomass to the sediments is shown by the high average chain length (ACL) of *n*-alkane ($>\text{C}_{25}$), indicative of a higher proportion of herb plants (Cui et al., 2015) (Fig. 1f-h).

The mean $\delta^{13}\text{C}_{\text{BOS}}$ value (-19.2‰) during the LGM was generally more positive than the upper limit of $\delta^{13}\text{C}$ of C_3 plants (i.e., -20‰) and therefore indicates that in-lake CO_2 utilized by phytoplankton at this time was derived from recycling of OM from C_4 plants (Fig. 1d). Recycling of C_4 plant detritus within the lake would also have shifted the dissolved carbon pool toward heavier isotope values (Street-Perrott et al., 1997). The observed enrichment in $\delta^{13}\text{C}_{\text{BOS}}$ is coeval with an increase in the abundance of alkaliphilous, benthic *Fragilaroid* diatoms

(*Pseudostaurosira brevistriata*, *Staurosira construens* f. *venter* and *Staurosirella pinnata*) (Fig. 1i) which support the inference of CO₂-limitation. Benthic *Fragilaria* are effective at utilizing HCO₃⁻ as a carbon source when CO₂ supply is limited (Sharkey and Berry, 1985).

When phytoplankton are scarce in the water column due to nutrient limitation, *Bosmina* has been shown to selectively graze flagellates as a higher quality food resource (DeMott and Kerfoot, 1982). Flagellates are typically mixotrophic and can utilize terrestrially-derived carbon via the microbial loop. Therefore, CO₂ resulting from mineralization of C₄-derived OM and its transfer to higher consumers may be the main factor influencing the positive $\delta^{13}\text{C}_{\text{BOS}}$ during the LGM even though t-OM inputs were very low. There is a strong offset between $\delta^{13}\text{C}$ of *Bosmina* and that of bulk organics at this time (Fig. 1d-e). $\delta^{13}\text{C}_{\text{BOS}}$ values are negatively correlated with both the sediment C accumulation rate and C/N ratio ($r = -0.79$, $P < 0.0001$; $r = -0.43$, $P < 0.05$, respectively) (Fig. 2b and d), suggesting that periods of low aquatic productivity are associated with $\delta^{13}\text{C}$ -enrichment (Matthews and Mazumder, 2006) (Fig. 1d).

Solar radiation output approached its maximum around 11 ka (Fig. 1a). Both bulk OM and *Bosmina* $\delta^{13}\text{C}$ decreased by ~ 1.5 – 2‰ in the period 18–11 ka (Fig. 1d and e) reflecting increasing atmospheric CO₂ (increased to $\sim 6.0 \mu\text{mol L}^{-1}$; Fig. 1c) and C₃ plant abundance in the catchment. Greater precipitation and warming are indicated by expansion of thermophilous forest taxa (e.g. *Betula*, *Carpinus*) and a sclerophyllous *Quercus* forest (Wang et al., 2014). The coupled lake-catchment became more productive, as shown by increased C burial rates (mean: $\sim 8.1 \text{ g C m}^{-2} \text{ yr}^{-1}$) and lake CO₂ (CO_{2aq}) increased to $1.9 \mu\text{mol L}^{-1}$. *Bosmina* production (as individuals $\text{cm}^{-2} \text{ yr}^{-1}$) increased during this period (Fig. 3c) and their accumulation is positively correlated with catchment tree cover ($r = 0.70$, $P < 0.0001$) throughout the record (Fig. 2f), indicating that conditions for zooplankton (warmer water, increased nutrient and food availability) were improving with expanding forest cover (Fig. 3d). Planktonic diatoms species composition and AR are also indicative of increasing nutrient transfer to the lake (Wang et al., 2014). The abundance of *n*-alkanes (C₂₃–C₃₁) of leaf waxes from higher plants increased from ~ 13 ka (Fig. 1f), suggesting expansion of terrestrial plants in the catchment.

The relationship between $\delta^{13}\text{C}_{\text{BOS}}$ and the $\delta^{18}\text{O}$ record from Dongge Cave (Fig. 2a; $r = 0.81$, $P < 0.0001$), primarily a measure of monsoonal intensity (Dykoski et al., 2005) suggests a positive but indirect climatic control of lake-carbon dynamics, via catchment hydrology. $\delta^{13}\text{C}_{\text{BOS}}$ oscillated between -30.7‰ and -25.9‰ after 10 ka (bulk organics were ca. -29‰) (Fig. 1e), which is similar to $\delta^{13}\text{C}$ of C₃ plants (-34.0‰ – -22.0‰) and depleted soil-derived organic matter (Deines, 1980; Gu et al., 2003). Present-day vegetation surrounding Lugu Lake has $\delta^{13}\text{C}$ of -29.0‰ to -26.0‰ based on measurements of the $\delta^{13}\text{C}$ of wetland and forest plants ($n = 10$) (Zhao, unpublished data) (See SI, Fig. S6). During the Holocene, vegetation with preference for warm and moist climate conditions, i.e. *Tusga* and *Alnus* (Fig. 3d) expanded and in-lake CO₂ would be increasingly derived from recycled t-OM (Jansson et al., 2007). *Bosmina*-inferred CO₂ reached $11.1 \mu\text{mol L}^{-1}$ during the mid-Holocene (Fig. 3a).

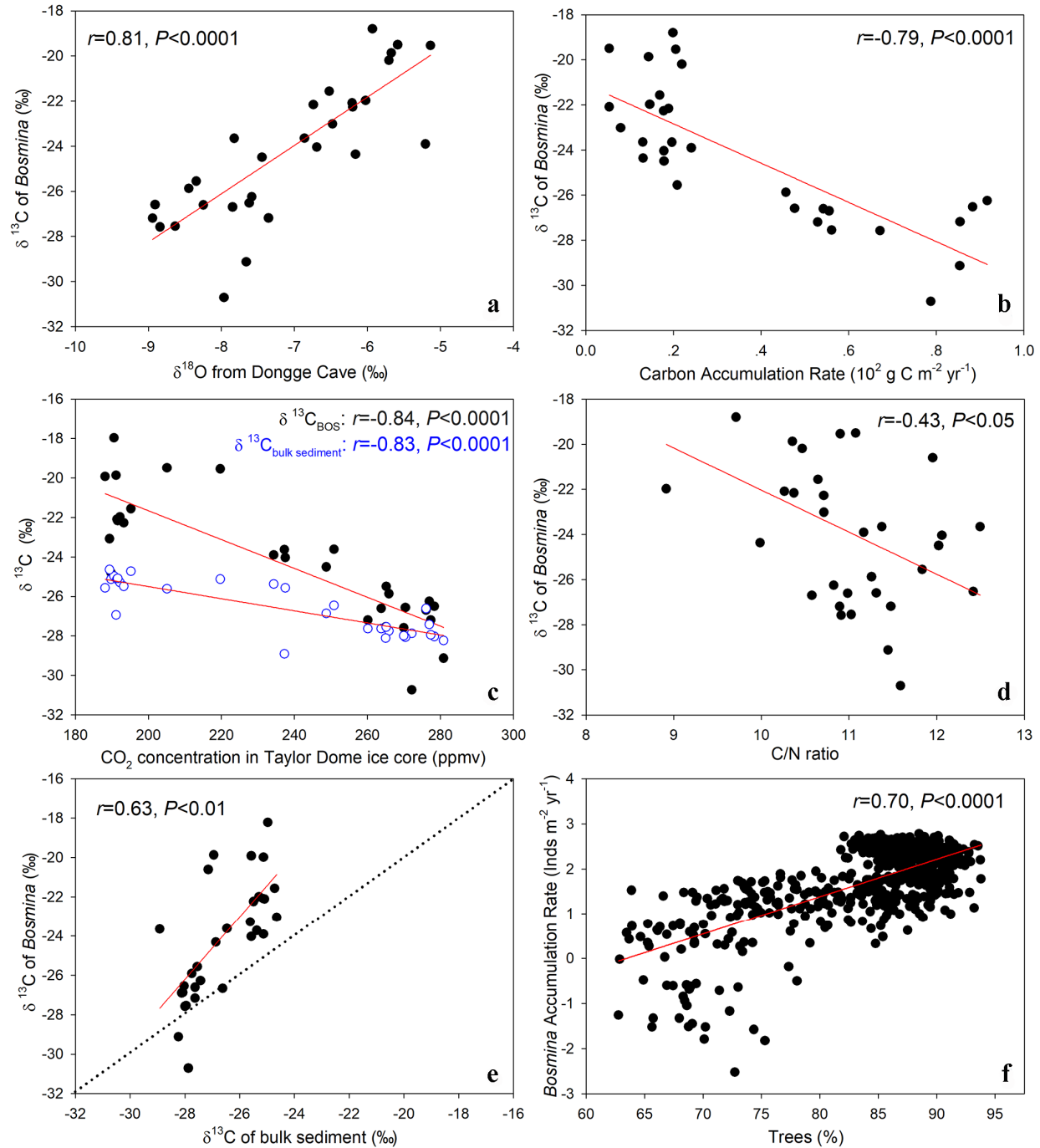


Fig. 2. The relationship between $\delta^{13}\text{C}$ of *Bosmina* and climate data and geochemical records. (a) Scatter plots of $\delta^{13}\text{C}$ of *Bosmina* from Lugu Lake versus $\delta^{18}\text{O}$ isotope from Dongge Cave, and (b) carbon accumulation rate (AR) of Lugu Lake. (c) *Bosmina* $\delta^{13}\text{C}$ and $\delta^{13}\text{C}$ of bulk sediments versus CO_2 concentration from Taylor Dome Ice Core (Smith et al., 1999). (d) *Bosmina* $\delta^{13}\text{C}$ versus C/N ratio from Lugu Lake, (e) *Bosmina* $\delta^{13}\text{C}$ versus $\delta^{13}\text{C}$ of bulk sediment from Lugu Lake, and (f) *Bosmina* accumulation rate versus the percentages of trees from Lugu Lake. The dotted line is the 1:1 line, while the red solid line represents the best-fit regression

line. The $\delta^{13}\text{C}$ isotope values of *Bosmina* in the most recent sediments are not included in the relationship.

3.3 CO₂ dynamics: atmosphere change

The $\delta^{13}\text{C}$ -*Bosmina*-CO₂ inference model provides an integration of terrestrial and aquatic ecosystem responses to environmental forcing since the LGM and indicates that the lake became supersaturated with respect to atmospheric CO₂ from 11 ka (Fig. 3a). In-lake CO₂ started to increase above its background value (2.9 $\mu\text{mol L}^{-1}$) from ~12 ka and atmosphere was 6.2 $\mu\text{mol L}^{-1}$ on average (Fig. 3a). Regional warming started around 15 ka at low latitudes (Shakun et al., 2012) but the increase in aquatic CO₂ (ca. 12 ka) only started with the strengthening of the SW monsoon (Dykoski et al., 2005; Overpeck et al., 1996) and the expansion of forest cover and ecosystem development (Figs. 1b and 3). Links between aquatic secondary producers, vegetation and carbon quality suggest hydrology and precipitation (monsoonal strength) not temperature were the primary drivers.

The monsoonal-driven C-balance that developed from 12 ka was disrupted by land-cover change associated with the start of early agriculture around 0.8 ka. This disturbance is clearly marked by a strong positive shift in $\delta^{13}\text{C}_{\text{BOS}}$ (to -15.3‰; Fig. 1d) possibly due to increased lake productivity and reduced discrimination against $\delta^{13}\text{C}$. Alternatively, these changes may have resulted in greater input of DIC from the catchment with positive $\delta^{13}\text{C}$ (Maberly et al., 2013). Land clearance for agriculture and disturbance of hydrological pathways is indicated by obvious increases in magnetic susceptibility, mean grain size, total algal production and changes in planktonic diatom species composition.

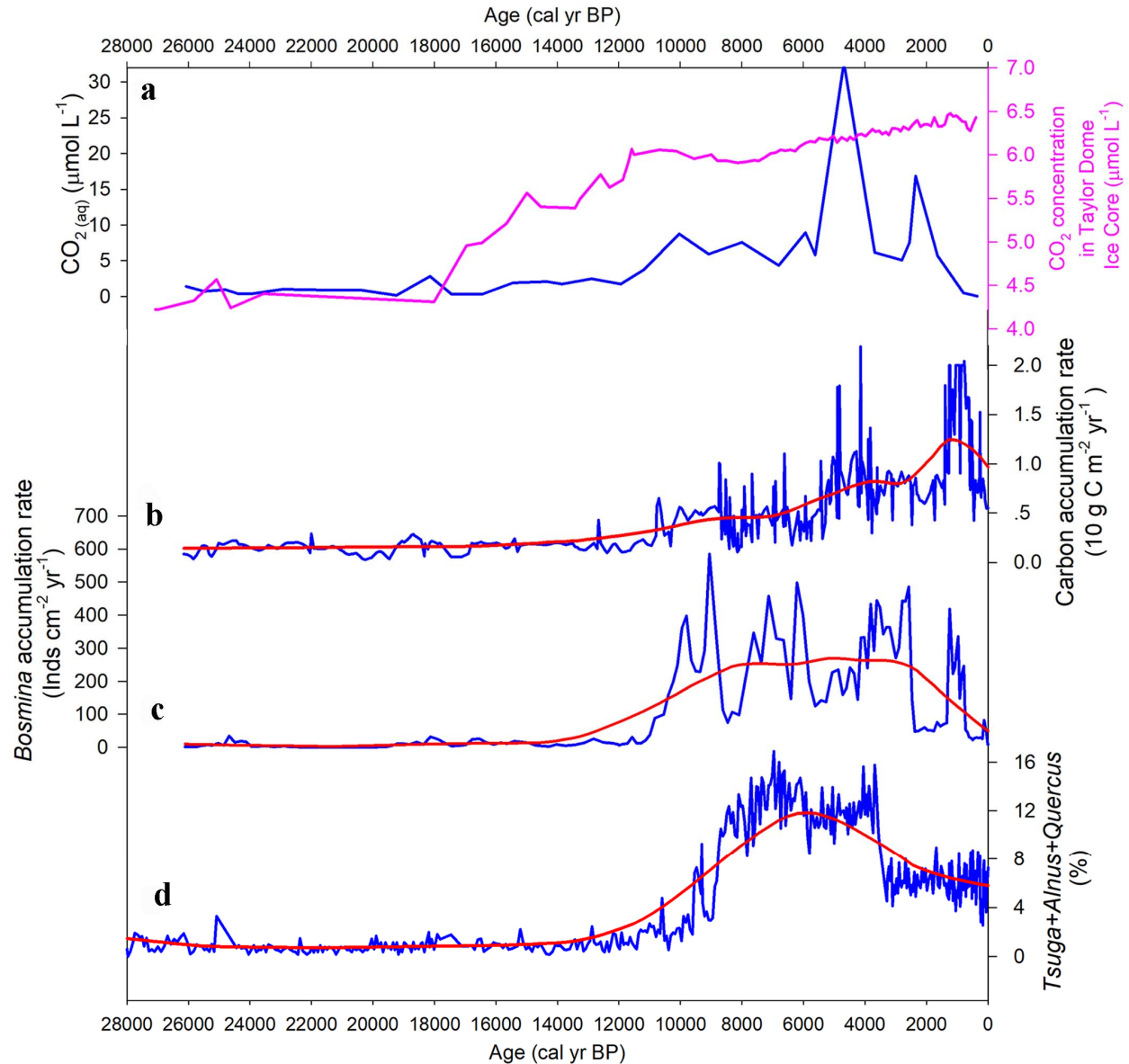


Fig. 3. Comparison of CO₂ concentrations data (a) and palaeolimnological records (b, c, d) from Lugu Lake, SW China. Fluctuations in (a) [CO_{2aq}] concentrations reconstructed from subfossil cladoceran $\delta^{13}\text{C}$ values using the model established in Smyntek, et al. (Smyntek et al., 2012), (b) carbon accumulation rate of Lugu Lake, (c) *Bosmina* accumulation rate of Lugu Lake and (d) total percentages of *Tsuga*, *Alnus* and *Quercus* from Lugu Lake over the last 25 ky. The fitted curves are loess smoothers (span 0.3, red lines).

4 Conclusions

This study shows that $\delta^{13}\text{C}_{\text{BOS}}$ can be used to reconstruct paleo-atmospheric $p\text{CO}_2$ over millennia and extends the timescale over which terrestrial subsidies can be considered (Tanentzap et al., 2017). During the LGM the low partial pressure of atmospheric CO₂ was a first order control on C dynamics in both the lake (which was undersaturated) and the catchment (where C₄ plants

dominated). The resultant CO₂-limitation during the LGM was reflected in the isotopic enrichment of $\delta^{13}\text{C}$ of *Bosmina*, relative to the $\delta^{13}\text{C}$ of bulk OM. As regional warming (from ~15 ka) predated increased zooplankton abundance, aquatic secondary production was dependent on forest expansion associated with the strengthening of the SW Monsoon some 3,000 yrs later. This lag highlights the important role of catchment vegetation changes and hydrological delivery of terrestrial OM and nutrients – indirect climate effects – play in driving the aquatic C balance. Given uncertainties about future trends in t-OM inputs to lakes (Creed et al., 2018), our results suggest that land-cover changes and altered precipitation patterns (both seasonality and amount) will influence aquatic C balances more than regional warming.

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