

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

Qian Wang<sup>1</sup>, John Anderson<sup>2</sup>, and Xiangdong Yang<sup>3</sup>

<sup>1</sup>Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences

<sup>2</sup>Loughborough University

<sup>3</sup>State Key Laboratory of Lake Science and Environment, Nanjing Institute of Geography and Limnology, Chinese Academy of Sciences

November 23, 2022

## Abstract

Lake metabolism and associated emissions of CO 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 CO and  $\delta\text{O}$  records of monsoonal strength (Dykoski et al., 2005; Wang et al., 2005) over the last ~26 kyr. The lake was CO-limited during the Last Glacial Maximum (LGM) when C vegetation dominated the catchment. Zooplankton production and inferred-lake CO (from  $\delta\text{C}$ ) 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 10-10 yr timescales.

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16 **Abstract**

17 Lake metabolism and associated emissions of CO<sub>2</sub> in lakes are heavily subsidized by terrestrial  
18 carbon but the role of climate forcing remains unclear. The carbon stable isotope composition of  
19 zooplankton in a sediment core from a sub-tropical alpine lake in SW China tracked atmospheric  
20 CO<sub>2</sub> and δ<sup>18</sup>O records of monsoonal strength (Dykoski et al., 2005; Wang et al., 2005) over the  
21 last ~26 kyr. The lake was CO<sub>2</sub>-limited during the Last Glacial Maximum (LGM) when C<sub>4</sub>  
22 vegetation dominated the catchment. Zooplankton production and inferred-lake CO<sub>2</sub> (from  
23 *Bosmina* δ<sup>13</sup>C) increased from 10 ka with strengthening of the SW Asian monsoon and forest  
24 expansion. These results highlight the importance of land-cover and hydrology in controlling  
25 terrestrial organic matter inputs to lakes and aquatic carbon dynamics at 10<sup>2</sup>-10<sup>3</sup> yr timescales.

26 **Plain Language Summary**

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

## 30 1 Introduction

31 Rising temperatures, altered hydrological pathways, and changes in land cover are resulting in  
32 fundamental changes in terrestrial-aquatic biogeochemical linkages (Creed et al., 2018). The  
33 carbon used by lake secondary producers (i.e. zooplankton) is a mixture between that fixed by  
34 aquatic primary producers and that transferred from catchment vegetation and soils, mainly as  
35 dissolved organic matter. The balance between the two sources depends on a range of factors  
36 (Tanentzap et al., 2017). However, any alteration in the supply of terrestrial carbon - the  
37 messenger between terrestrial and lake ecosystems (Creed et al., 2018) - has potentially profound  
38 effects on the structure and function of lakes and the emission of greenhouse gases. Terrestrially-  
39 derived organic material (t-OM) supports secondary production in lakes (Pace et al., 2004) but its  
40 role remains contentious (Grey and Jones, 2001; Tanentzap et al., 2017). It has been argued that  
41 t-OM is especially important in sustaining zooplankton in lakes that have low primary  
42 production (Carpenter et al., 2005). The amount of t-OM imported from the catchment may be  
43 several orders of magnitude higher than the amount of autochthonous OC that is generated inside  
44 the lake with resultant net CO<sub>2</sub> emissions from lakes (Sobek et al., 2003). The terrestrial subsidy  
45 to aquatic food webs can also stabilize population dynamics and predator-prey interactions and  
46 influence carbon emissions by lakes (Schindler, 1997). The balance between these auto- and  
47 heterotrophic C sources (primary production and respiration) varies both seasonally and over  
48 longer timescales (del Giorgio and France, 1996). How these linkages will be altered with both  
49 changing climate (precipitation as well as temperature) and land-cover is, however, unclear.

50 Terrestrial contributions to zooplankton have been estimated primarily by using zooplankton  
51 carbon stable isotopes ( $\delta^{13}\text{C}$ ) (Grey and Jones, 2001) which closely reflect their diet (Fry and  
52 Sherr, 1984). It has also been shown to provide a measure of the baseline pelagic  $\delta^{13}\text{C}$  of a lake  
53 (Smyntek et al., 2012) and the possibility of reconstructing aquatic CO<sub>2</sub> over timescales much  
54 longer than those covered by monitoring (Perga et al., 2016). Although many studies to date  
55 suggest significant use of t-OM by zooplankton, how its use varies in response to climate change  
56 is unclear, if only because of the widespread human impact on land-cover (Ellis et al., 2013)  
57 which confound climate signals in contemporary studies (Creed et al., 2018; Tanentzap et al.,  
58 2017).

59 Precipitation influences terrestrial-aquatic linkages and t-OM supply rates (Tranvik et al., 2009)  
60 and disentangling the role of terrestrial C against a background of climate change is crucial for  
61 understanding their interaction in the future. To date, much of the evidence for the effects of t-  
62 OM inputs is derived from spatial surveys and experiments in the temperate-boreal zone (Grey  
63 and Jones, 2001; Tanentzap et al., 2017). Alternatively, palaeoecological methods can be used to  
64 understand interactions at one site prior to the onset of anthropogenic landscape change. Here we  
65 used a multi-proxy palaeolimnological approach and inferred in-lake CO<sub>2</sub> from  $\delta^{13}\text{C}$  of *Bosmina*  
66 ( $\delta^{13}\text{C}_{\text{BOS}}$ ) (Perga et al., 2016) to test the hypothesis that zooplankton production and CO<sub>2</sub>  
67 dynamics in a large, deep sub-tropical lake (Lugu Lake, SW China) reflect climate-driven  
68 terrestrial subsidies since the Last Glacial Maximum (LGM, ~26 kyr).

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

72 primarily an herbivore, consuming phytoplankton (an assumption of the use of  $\delta^{13}\text{C}_{\text{BOS}}$  to infer  
73 lake-water  $\text{CO}_2$  (See SI and Perga et al. (2016) for a discussion).

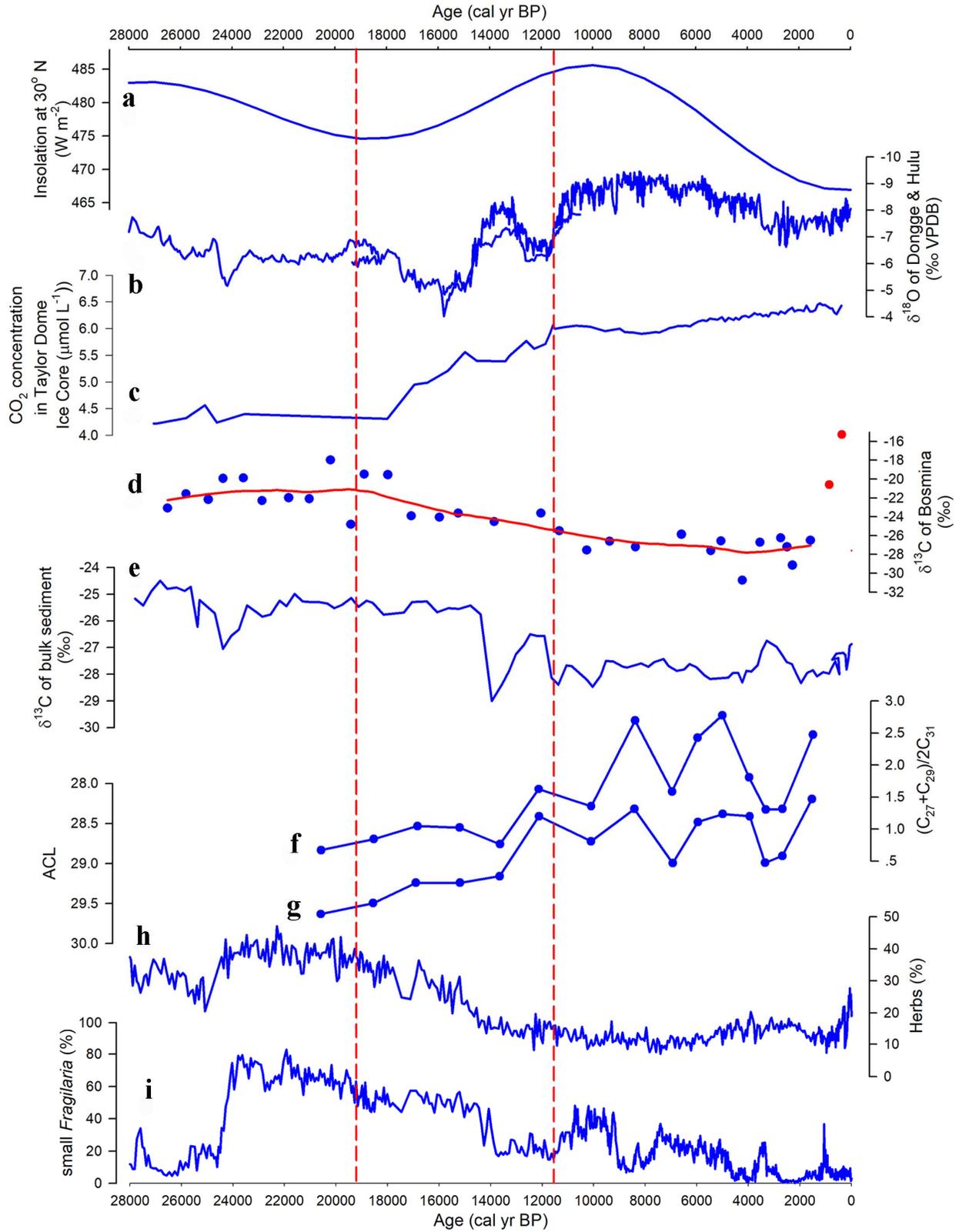
## 74 **2 Materials and Methods**

### 75 2.1 Zooplankton stable isotope analyses

76 To extract sufficient numbers of cladoceran subfossil, a total of 32 subsamples, from 0-  
77 164 cm, 164-288 cm, 288-418 cm, 418-554 cm, 554-770 cm and 770-830 cm, were taken  
78 from Lugu sediment core. They are clusters of three samples at different depths. Isotope  
79 analyses were performed only on *Bosmina* remains, as *Bosmina* remains were abundant  
80 enough (abundances >80%). Freeze-dried cladoceran samples were heated for 30 min in  
81 KOH 10% at 70 °C in order to dissolve the organic labile constituents. Samples were then  
82 rinsed with deionized water, transferred in a beaker with HCL 10% for 5 min to remove  
83 carbonates (Nevalainen et al., 2014). Samples were rinsed one more time. *Bosmina*  
84 remains (head shields and carapaces) were sieved with 32- $\mu\text{m}$  filter and thoroughly  
85 rinsed. The remaining materials were *Bosmina* exoskeletons. Exoskeletons were then  
86 sorted under a dissecting microscope and packed into tin cups in order to reach 0.2 mg  
87 dry weight (Perga, 2010). Previous experiments performed on cladoceran subfossil  
88 remains have demonstrated that these chemical treatments and taphonomic processes  
89 have minor effects on the  $\delta^{13}\text{C}$  values obtained for the remains (Perga, 2011). C stable  
90 isotope composition was measured from Deltaplus mass spectrometer (Thermo Fisher  
91 Scientific Inc., West Palm Beach, FL, USA). Their composition was expressed in the  
92 conventional  $\delta$  notation, defined as per mil (‰) deviation against VPDB.

### 93 2.2 Calibration of the paleoproxy for $\text{CO}_{2\text{aq}}$

94 The seasonal data for cladoceran  $\delta^{13}\text{C}$  values were available and dissolved  $\text{CO}_2$   
95 concentrations ( $\text{CO}_{2\text{aq}}$ ) (as the sum of dissolved  $\text{CO}_2$  and  $\text{H}_2\text{CO}_3$ ) in the water column  
96 was calculated following Stumm and Morgan (1995), accounting for lake water pH,  
97 temperature, and DIC concentrations (Cole et al., 1994) using Visual MINTEQ version  
98 3.1 (Gustaffson, 2013). A log linear regression model linking surface lake  $\text{CO}_2$   
99 concentrations and *Bosmina*  $\delta^{13}\text{C}$  values was computed from the Lugu Lake seasonal  
100 monitoring data set and compared with a model previously developed for Windermere  
101 (Smyntek et al., 2012). As in Perga et al. (2016), we tested the ability of the model to  
102 predict past  $\text{CO}_2$  concentrations using monitoring data. The  $\text{CO}_2$  concentrations from the  
103 water columns over the last 26 kyr were reconstructed from subfossil cladoceran  $\delta^{13}\text{C}$   
104 values using the model established in Smyntek et al. (2012).



106 **Fig. 1. Comparisons of the regional and local records around Lugu Lake during the last 28**  
 107 **ka.** (a) Solar insolation (July) at 30° N (Berger and Loutre, 1991). (b)  $\delta^{18}\text{O}$  data from Dongge  
 108 and Hulu Cave (Dykoski et al., 2005; Wang et al., 2001). (c)  $\text{CO}_2$  concentration from Taylor  
 109 Dome Ice Core (Smith et al., 1999). (d)  $\delta^{13}\text{C}$  of *Bosmina* from Lugu Lake. (e)  $\delta^{13}\text{C}$  of bulk  
 110 sediment from Lugu Lake. (f) *n*-alkanes parameters:  $(\text{C}_{27}+\text{C}_{29})/2\text{C}_{31}$  and (g) average carbon  
 111 length (ACL) from Lugu Lake. (h) Percentages of herbs from Lugu Lake. (i) Percentages of  
 112 small benthic *Fragilaria* from Lugu Lake. The fitted curves are loess smoothers (span 0.3, red  
 113 lines).

### 114 3 Results and Discussion

#### 115 3.1 *Bosmina* dominance during 26 ka

116 With the exception of the period 22–19 ka (years before the present, where the “present” is  
 117 defined as the year 1950 A.D.; see Supplementary Information), the zooplankton community at  
 118 Lugu Lake was dominated by the pelagic cladoceran *Bosmina* [(*Eubosmina coregoni*, *B.*  
 119 *longispina*, and *B. longirostris*] for more than 20 kyr (Fig. S4). The total cladoceran  
 120 accumulation rate (AR) was extremely low during the LGM but the abundance and AR of  
 121 pelagic *Bosmina* taxa showed an abrupt increase after 18 ka and reached  $\sim 600$  inds  $\text{cm}^{-2} \text{yr}^{-1}$   
 122 around 11 ka (Fig. S4). The  $\delta^{13}\text{C}$  of bulk sediment ( $\text{OM}_{\text{sed}}$ ) ranged from  $-27.0\text{‰}$  to  $-24.5\text{‰}$ , and  
 123 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).  
 124 In contrast, the  $\delta^{13}\text{C}_{\text{BOS}}$  was enriched up to  $-18\text{‰}$  and the greatest differences between  $\text{OM}_{\text{sed}}$   
 125 and *Bosmina*  $\delta^{13}\text{C}$  occur at this time ( $\sim 4\text{‰}$ ) (Fig. 1d and e).

#### 126 3.2 Terrestrial input during the Last Glacial cycle

127  $\delta^{13}\text{C}_{\text{BOS}}$  tracks atmospheric  $\text{CO}_2$  concentration recorded in the Taylor Dome ice core (Smith et  
 128 al., 1999) ( $r=0.72$ ,  $P<0.0001$ ; Fig. 1b, c and Fig. 2c). A *Bosmina*- $\text{CO}_2$  inference model suggests  
 129 that the lake was under-saturated with respect to atmospheric  $\text{CO}_2$  ( $1.0 \mu\text{mol L}^{-1}$  versus  $4.7 \mu\text{mol}$   
 130  $\text{L}^{-1}$ ). The climate around Lugu Lake during the LGM was dry and cold, perhaps  $\sim 5\text{--}6 \text{ }^\circ\text{C}$  cooler  
 131 than today. The increased aridity and low atmospheric  $\text{CO}_2$  concentration drove an expansion of  
 132  $\text{C}_4$  plants (e.g., *Artemisia*, *Cyperaceae*) during the LGM around Lugu Lake as observed  
 133 elsewhere (Ehleringer et al., 1997; Street-Perrott et al., 1997).  $\text{C}_4$  plants possess a  $\text{CO}_2$   
 134 concentrating mechanism and have low levels of respiratory inhibition of photosynthesis  
 135 (Farquhar et al., 1989), and so have an important advantage over  $\text{C}_3$  plants at times of low  
 136 atmospheric  $\text{CO}_2$  partial pressure ( $p\text{CO}_2$ )/ $\text{O}_2$  ratios (Sage, 2001). The  $\text{C}_4$  pathway characteristic  
 137 of herbs leads to  $\delta^{13}\text{C}$  values between  $-17\text{‰}$  and  $-9\text{‰}$  while  $\text{C}_3$  plants range from  $-32\text{‰}$  to  
 138  $-20\text{‰}$  (Deines, 1980). The enhanced contribution of  $\text{C}_4$  plant biomass to the sediments is shown  
 139 by the high average chain length (ACL) of *n*-alkane ( $>\text{C}_{25}$ ), indicative of a higher proportion of  
 140 herb plants (Cui et al., 2015) (Fig. 1f-h).

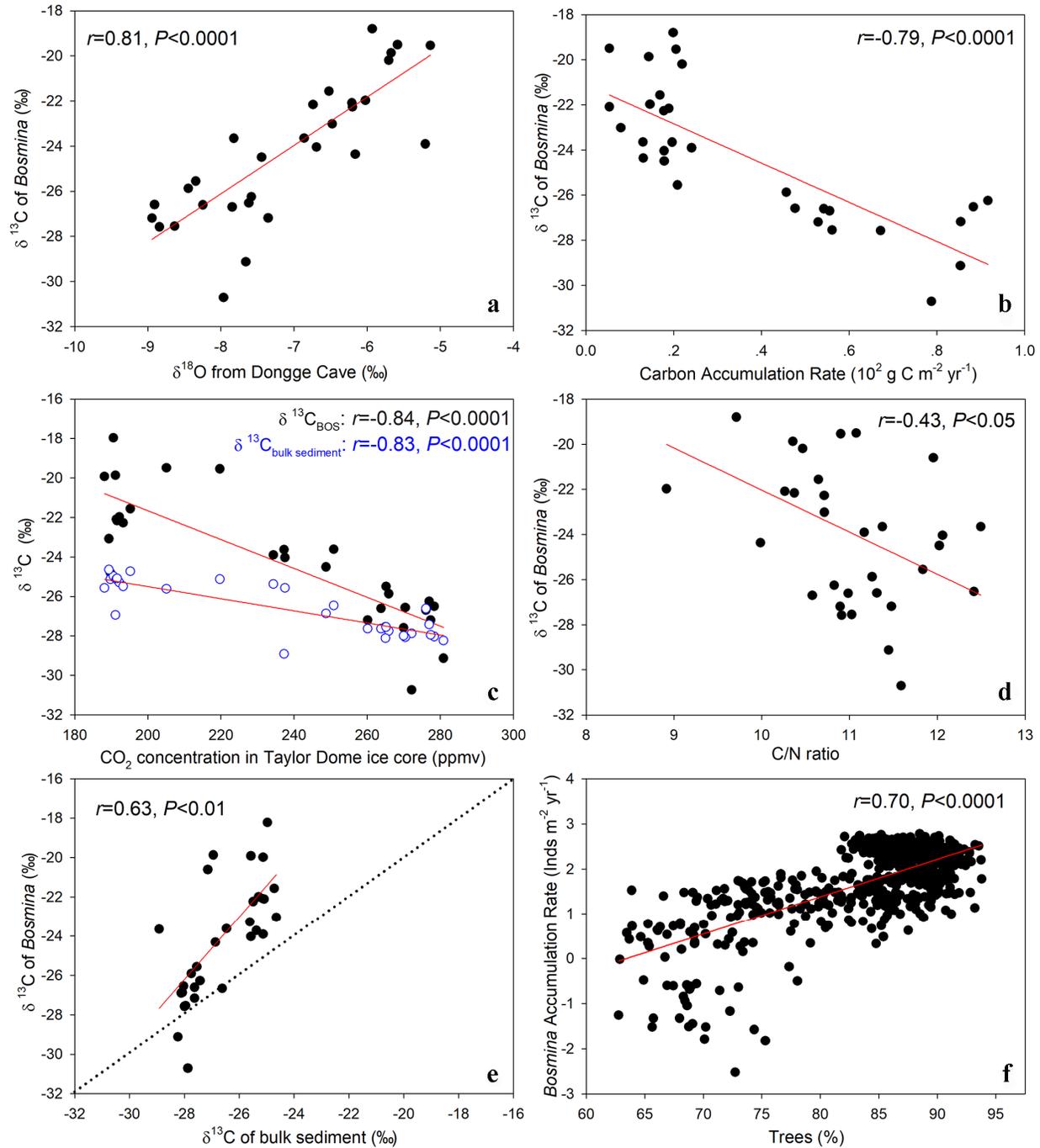
141 The mean  $\delta^{13}\text{C}_{\text{BOS}}$  value ( $-19.2\text{‰}$ ) during the LGM was generally more positive than the upper  
 142 limit of  $\delta^{13}\text{C}$  of  $\text{C}_3$  plants (i.e.,  $-20\text{‰}$ ) and therefore indicates that in-lake  $\text{CO}_2$  utilized by  
 143 phytoplankton at this time was derived from recycling of OM from  $\text{C}_4$  plants (Fig. 1d).  
 144 Recycling of  $\text{C}_4$  plant detritus within the lake would also have shifted the dissolved carbon pool  
 145 toward heavier isotope values (Street-Perrott et al., 1997). The observed enrichment in  $\delta^{13}\text{C}_{\text{BOS}}$  is  
 146 coeval with an increase in the abundance of alkaliphilous, benthic Fragilaroid diatoms

147 (*Pseudostaurosira brevistriata*, *Staurosira construens* f. *venter* and *Staurosirella pinnata*) (Fig.  
 148 1i) which support the inference of CO<sub>2</sub>-limitation. Benthic *Fragilaria* are effective at utilizing  
 149 HCO<sub>3</sub><sup>-</sup> as a carbon source when CO<sub>2</sub> supply is limited (Sharkey and Berry, 1985).

150 When phytoplankton are scarce in the water column due to nutrient limitation, *Bosmina* has been  
 151 shown to selectively graze flagellates as a higher quality food resource (DeMott and Kerfoot,  
 152 1982). Flagellates are typically mixotrophic and can utilize terrestrially-derived carbon via the  
 153 microbial loop. Therefore, CO<sub>2</sub> resulting from mineralization of C<sub>4</sub>-derived OM and its transfer  
 154 to higher consumers may be the main factor influencing the positive δ<sup>13</sup>C<sub>BOS</sub> during the LGM  
 155 even though t-OM inputs were very low. There is a strong offset between δ<sup>13</sup>C of *Bosmina* and  
 156 that of bulk organics at this time (Fig. 1d-e). δ<sup>13</sup>C<sub>BOS</sub> values are negatively correlated with both  
 157 the sediment C accumulation rate and C/N ratio ( $r = -0.79$ ,  $P < 0.0001$ ;  $r = -0.43$ ,  $P < 0.05$ ,  
 158 respectively) (Fig. 2b and d), suggesting that periods of low aquatic productivity are associated  
 159 with δ<sup>13</sup>C-enrichment (Matthews and Mazumder, 2006) (Fig. 1d).

160 Solar radiation output approached its maximum around 11 ka (Fig. 1a). Both bulk OM and  
 161 *Bosmina* δ<sup>13</sup>C decreased by ~1.5–2‰ in the period 18–11 ka (Fig. 1d and e) reflecting increasing  
 162 atmospheric CO<sub>2</sub> (increased to ~6.0 μmol L<sup>-1</sup>; Fig. 1c) and C<sub>3</sub> plant abundance in the catchment.  
 163 Greater precipitation and warming are indicated by expansion of thermophilous forest taxa (e.g.  
 164 *Betula*, *Carpinus*) and a sclerophyllous *Quercus* forest (Wang et al., 2014). The coupled lake-  
 165 catchment became more productive, as shown by increased C burial rates (mean: ~8.1 g C m<sup>-2</sup> yr<sup>-1</sup>)  
 166 and lake CO<sub>2</sub> (CO<sub>2aq</sub>) increased to 1.9 μmol L<sup>-1</sup>. *Bosmina* production (as individuals cm<sup>-2</sup> yr<sup>-1</sup>)  
 167 increased during this period (Fig. 3c) and their accumulation is positively correlated with  
 168 catchment tree cover ( $r = 0.70$ ,  $P < 0.0001$ ) throughout the record (Fig. 2f), indicating that  
 169 conditions for zooplankton (warmer water, increased nutrient and food availability) were  
 170 improving with expanding forest cover (Fig. 3d). Planktonic diatoms species composition and  
 171 AR are also indicative of increasing nutrient transfer to the lake (Wang et al., 2014). The  
 172 abundance of *n*-alkanes (C<sub>23</sub>-C<sub>31</sub>) of leaf waxes from higher plants increased from ~13 ka (Fig.  
 173 1f), suggesting expansion of terrestrial plants in the catchment.

174 The relationship between δ<sup>13</sup>C<sub>BOS</sub> and the δ<sup>18</sup>O record from Dongge Cave (Fig. 2a;  $r = 0.81$ ,  
 175  $P < 0.0001$ ), primarily a measure of monsoonal intensity (Dykoski et al., 2005) suggests a positive  
 176 but indirect climatic control of lake-carbon dynamics, via catchment hydrology. δ<sup>13</sup>C<sub>BOS</sub>  
 177 oscillated between -30.7‰ and -25.9‰ after 10 ka (bulk organics were ca. -29‰) (Fig. 1e),  
 178 which is similar to δ<sup>13</sup>C of C<sub>3</sub> plants (-34.0‰~-22.0‰) and depleted soil-derived organic matter  
 179 (Deines, 1980; Gu et al., 2003). Present-day vegetation surrounding Lugu Lake has δ<sup>13</sup>C of  
 180 -29.0‰ to -26.0‰ based on measurements of the δ<sup>13</sup>C of wetland and forest plants ( $n = 10$ )  
 181 (Zhao, unpublished data) (See SI, Fig. S6). During the Holocene, vegetation with preference for  
 182 warm and moist climate conditions, i.e. *Tusga* and *Alnus* (Fig. 3d) expanded and in-lake CO<sub>2</sub>  
 183 would be increasingly derived from recycled t-OM (Jansson et al., 2007). *Bosmina*-inferred CO<sub>2</sub>  
 184 reached 11.1 μmol L<sup>-1</sup> during the mid-Holocene (Fig. 3a).



185

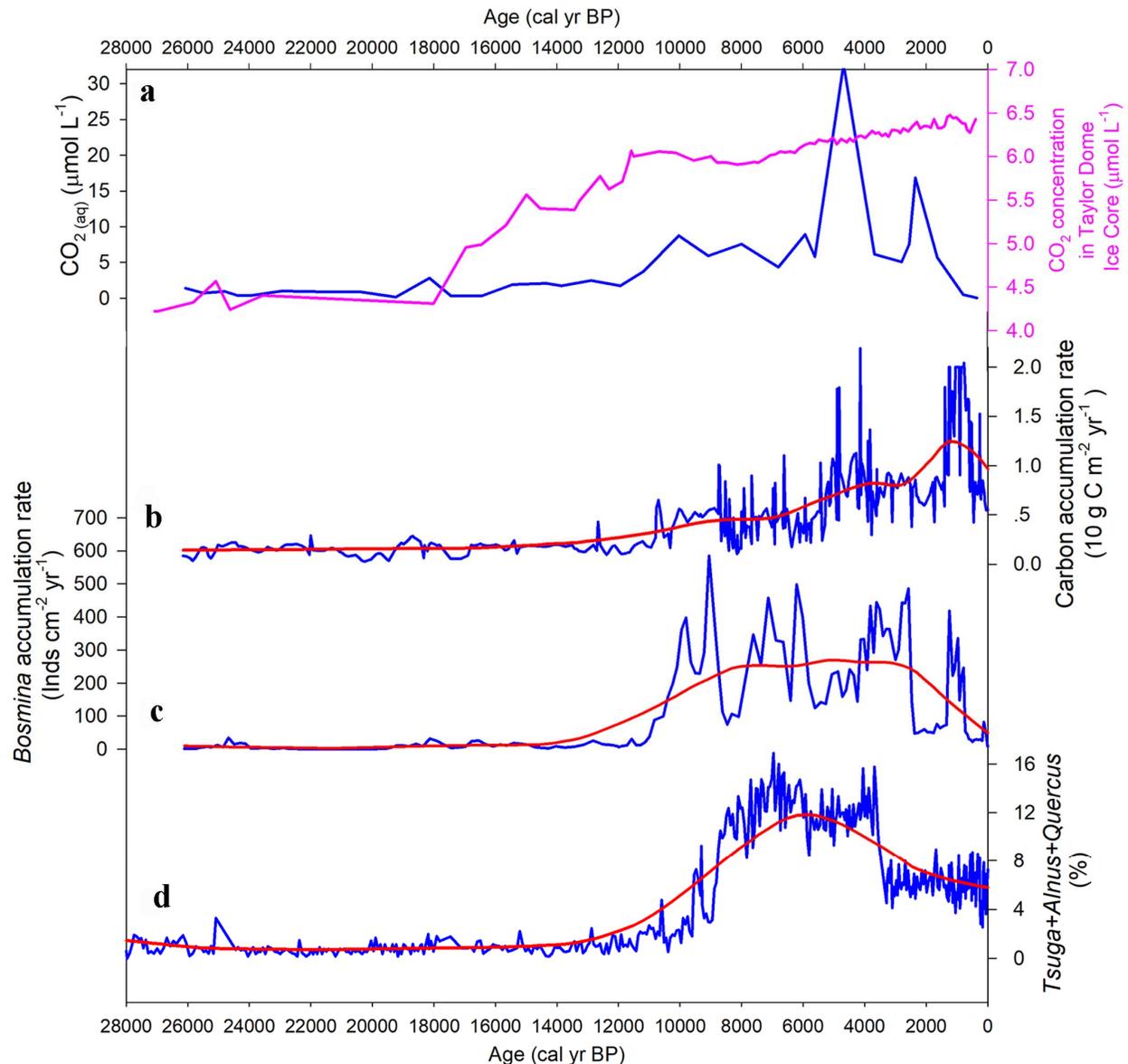
186 **Fig. 2. The relationship between  $\delta^{13}\text{C}$  of *Bosmina* and climate data and geochemical**  
 187 **records.** (a) Scatter plots of  $\delta^{13}\text{C}$  of *Bosmina* from Lugu Lake versus  $\delta^{18}\text{O}$  isotope from Dongge  
 188 Cave, and (b) carbon accumulation rate (AR) of Lugu Lake. (c) *Bosmina*  $\delta^{13}\text{C}$  and  $\delta^{13}\text{C}$  of bulk  
 189 sediments versus  $\text{CO}_2$  concentration from Taylor Dome Ice Core (Smith et al., 1999). (d)  
 190 *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  
 191 from Lugu Lake, and (f) *Bosmina* accumulation rate versus the percentages of trees from Lugu  
 192 Lake. The dotted line is the 1:1 line, while the red solid line represents the best-fit regression

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

### 195 **3.3 CO<sub>2</sub> dynamics: atmosphere change**

196 The  $\delta^{13}\text{C}$ -*Bosmina*-CO<sub>2</sub> inference model provides an integration of terrestrial and aquatic  
197 ecosystem responses to environmental forcing since the LGM and indicates that the lake became  
198 supersaturated with respect to atmospheric CO<sub>2</sub> from 11 ka (Fig. 3a). In-lake CO<sub>2</sub> started to  
199 increase above its background value (2.9  $\mu\text{mol L}^{-1}$ ) from ~12 ka and atmosphere was 6.2  $\mu\text{mol L}^{-1}$   
200 on average (Fig. 3a). Regional warming started around 15 ka at low latitudes (Shakun et al.,  
201 2012) but the increase in aquatic CO<sub>2</sub> (ca. 12 ka) only started with the strengthening of the SW  
202 monsoon (Dykoski et al., 2005; Overpeck et al., 1996) and the expansion of forest cover and  
203 ecosystem development (Figs. 1b and 3). Links between aquatic secondary producers, vegetation  
204 and carbon quality suggest hydrology and precipitation (monsoonal strength) not temperature  
205 were the primary drivers.

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



214

215 **Fig. 3. Comparison of CO<sub>2</sub> concentrations data (a) and palaeolimnological records (b, c, d)**  
 216 **from Lugu Lake, SW China.** Fluctuations in (a) [CO<sub>2aq</sub>] concentrations reconstructed from  
 217 subfossil cladoceran δ<sup>13</sup>C values using the model established in Smyntek, et al. (Smyntek et al.,  
 218 2012), (b) carbon accumulation rate of Lugu Lake, (c) *Bosmina* accumulation rate of Lugu Lake  
 219 and (d) total percentages of *Tsuga*, *Alnus* and *Quercus* from Lugu Lake over the last 25 ky. The  
 220 fitted curves are loess smoothers (span 0.3, red lines).

## 221 4 Conclusions

222 This study shows that δ<sup>13</sup>C<sub>BOS</sub> can be used to reconstruct paleo-atmospheric *p*CO<sub>2</sub> over millennia  
 223 and extends the timescale over which terrestrial subsidies can be considered (Tanentzap et al.,  
 224 2017). During the LGM the low partial pressure of atmospheric CO<sub>2</sub> was a first order control on  
 225 C dynamics in both the lake (which was undersaturated) and the catchment (where C<sub>4</sub> plants

226 dominated). The resultant CO<sub>2</sub>-limitation during the LGM was reflected in the isotopic  
 227 enrichment of  $\delta^{13}\text{C}$  of *Bosmina*, relative to the  $\delta^{13}\text{C}$  of bulk OM. As regional warming (from ~15  
 228 ka) predated increased zooplankton abundance, aquatic secondary production was dependent on  
 229 forest expansion associated with the strengthening of the SW Monsoon some 3,000 yrs later.  
 230 This lag highlights the important role of catchment vegetation changes and hydrological delivery  
 231 of terrestrial OM and nutrients – indirect climate effects – play in driving the aquatic C balance.  
 232 Given uncertainties about future trends in t-OM inputs to lakes (Creed et al., 2018), our results  
 233 suggest that land-cover changes and altered precipitation patterns (both seasonality and amount)  
 234 will influence aquatic C balances more than regional warming.

## 235 Acknowledgments

236 We thank Rong Wang for his helpful discussions and suggestions during the preparation of the  
 237 manuscript. All results are reported in the main text and supplementary materials. This work was  
 238 supported by the National Key Research and Development Program of China  
 239 (2016YFA0600502) and the National Natural Science Foundation of China (41877439,  
 240 41502170, 41302277, and 41807446). The LG-13C data are deposited in repository  
 241 (<https://doi.org/10.4121/uuid:7dbcdf9f-ea8d-4130-bf23-afc397ef5ce2>).

## 242 References

- 243 Berger, S. A., & Loutre, M. F. (1991). Insolation values for the climate of the last 10 million years, *Quaternary*  
 244 *Science Reviews*, *10*, 297–317.
- 245 Carpenter, S. R., Cole, J. J., Pace, M. L., Van de Bogert, M. C., Bade, D. L., Bastviken, D., et al. (2005). Ecosystem  
 246 subsidies: Terrestrial support of aquatic food webs from <sup>13</sup>C addition to contrasting lakes, *Ecology*, *86*(10),  
 247 2737–2750. <https://doi.org/10.1890/04-1282>.
- 248 Cole, J. J., Caraco, N. F., Kling, G. W., & Kratz, T. K. (1994). Carbon Dioxide Supersaturation in the Surface  
 249 Waters of Lakes, *Science*, *265*(5178), 1568–1570. <https://doi.org/10.1126/science.265.5178.1568>.
- 250 Creed, I. F., Bergstrom, A. K., Trick, C. G., Grimm, N. B., Hessen, D. O., Karlsson, J., et al. (2018). Global change-  
 251 driven effects on dissolved organic matter composition: Implications for food webs of northern lakes, *Glob Chang*  
 252 *Biol*, *24*(8), 3692–3714. <https://doi.org/10.1111/gcb.14129>.
- 253 Cui, L. L., Wang, X., Shen, J., & Ding, Z. L. (2015). Changes in distribution and compound-specific carbon isotope  
 254 compositions of *n*-alkanes as recorded in Lugu Lake sediments from Southwest China since Last Glacial Maximum  
 255 and implications for paleovegetation evolution, *Quaternary Sciences*, *35*(4), 871–880 (in Chinese).
- 256 Deines, P. (1980). The isotopic composition of reduced organic carbon, in *Handbook of Environmental Isotope*  
 257 *Geochemistry*, edited by Fritz, P. & Fontes, J. C., p. 326–406, Elsevier, Netherlands.
- 258 del Giorgio, P. A., & France, R. I. (1996). Ecosystem-specific patterns in the relationship between zooplankton and  
 259 POM or microplankton  $\delta^{13}\text{C}$ , *Limnology and Oceanography*, *41*(2), 359–365.  
 260 <https://doi.org/10.4319/lo.1996.41.2.0359>.
- 261 DeMott, W. R., & Kerfoot, W. C. (1982). Competition among cladocerans: Nature of the interaction between  
 262 *Bosmina* and *Daphnia*, *Ecology*, *63*(6), 1949–1966. <https://doi.org/10.2307/1940132>.
- 263 Dykoski, C., Edwards, R., Cheng, H., Yuan, D., Cai, Y., Zhang, M., et al. (2005). A high-resolution, absolute-dated  
 264 Holocene and deglacial Asian monsoon record from Dongge Cave, China, *Earth and Planetary Science Letters*,  
 265 *233*(1–2), 71–86. <https://doi.org/10.1016/j.epsl.2005.01.036>.
- 266 Ehleringer, J. R., Cerling, T. E., & Helliker, B. R. (1997). C<sub>4</sub> photosynthesis, atmospheric CO<sub>2</sub>, and climate,  
 267 *Oecologia*, *112*, 285–299. <https://doi.org/10.1007/s004420050311>.
- 268 Ellis, E. C., Kaplan, J. O., Fuller, D. Q., Vavrus, S., Klein Goldewijk, K., & Verburg, P. H. (2013). Used planet: a  
 269 global history, *Proceedings of the National Academy of Sciences of the United States of America*, *110*(20),  
 270 7978–7985. <https://doi.org/10.1073/pnas.1217241110>.
- 271 Farquhar, G. D., Ehleringer, J. R., & Hubick, K. T. (1989). Carbon isotope discrimination and photosynthesis,  
 272 *Annual Review Of Plant Physiology and Plant Molecular Biology*, *40*, 503–537.
- 273 Fry, B., & Sherr, E. B. (1984).  $\delta^{13}\text{C}$  measurements as indicators of carbon flow in marine and freshwater  
 274 ecosystems, *Ecological Studies*, 196–229. [https://doi.org/10.1007/978-1-4612-3498-2\\_12](https://doi.org/10.1007/978-1-4612-3498-2_12).

- 275 Grey, J., & Jones, R. I. (2001). Seasonal changes in the importance of the source of organic matter to the diet of  
276 zooplankton in Loch Ness, as indicated by stable isotope analysis, *Limnology and Oceanography*, 46(3), 505–513.  
277 <https://doi.org/10.4319/lo.2001.46.3.0505>.
- 278 Gu, Z., Liu, Q., Xu, B., Han, J., Yang, S., Ding, Z., et al. (2003). Climate as the dominant control on C<sub>3</sub> and C<sub>4</sub> plant  
279 abundance in the Loess Plateau: Organic carbon isotope evidence from the last glacial-interglacial loess-soil  
280 sequences, *Chinese Science Bulletin*, 48(12), 1271–1276. <https://doi.org/10.1360/03wd0200>.
- 281 Gustaffson, J. P. (2013). Visual MINTEQ Ver. 3.1, edited, p. <https://vminteq.lwr.kth.se/>.
- 282 Jansson, M., Persson, L., De Roos, A. M., Jones, R. I., & Tranvik, L. J. (2007). Terrestrial carbon and intraspecific  
283 size-variation shape lake ecosystems, *Trends in Ecology and Evolution*, 22(6), 316–322.  
284 <https://doi.org/10.1016/j.tree.2007.02.015>.
- 285 Maberly, S. C., Barker, P. A., Stott, A. W., & De Ville, M. M. (2013). Catchment productivity controls CO<sub>2</sub>  
286 emissions from lakes, *Nature Climate Change*, 3(4), 391–394. <https://doi.org/10.1038/nclimate1748>.
- 287 Matthews, B., & Mazumder, A. (2006). Habitat specialization and the exploitation of allochthonous carbon by  
288 zooplankton, *Ecology*, 87(11), 2800–2812. [https://doi.org/10.1890/0012-9658\(2006\)87\[2800:HSATEO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2006)87[2800:HSATEO]2.0.CO;2).
- 289 Nevalainen, L., Luoto, T. P., Manca, M., & Weisse, T. (2014). A paleolimnological perspective on aquatic  
290 biodiversity in Austrian mountain lakes, *Aquatic Sciences*, 77(1), 59–69. 10.1007/s00027-014-0363-6.
- 291 Overpeck, J., Anderson, D., Trumbore, S., & Prell, W. (1996). The southwest Indian Monsoon over the last 18000  
292 years, *Climate Dynamics*, 12, 213–225. <https://doi.org/10.1007/BF00211619>.
- 293 Pace, M. L., Cole, J. J., Carpenter, S. R., Kitchell, J. F., Hodgson, J. R., Bogert, M. C. V. d., et al. (2004). Whole-  
294 lake carbon-13 additions reveal terrestrial support of aquatic food webs, *Nature*, 427, 240–243.  
295 <https://doi.org/10.1038/nature02215>.
- 296 Perga, M. E. (2010). Potential of  $\delta^{13}\text{C}$  and  $\delta^{15}\text{N}$  of cladoceran subfossil exoskeletons for paleo-ecological studies,  
297 *Journal Of Paleolimnology*, 44(2), 387–395. <https://doi.org/10.1007/s10933-009-9340-9>.
- 298 Perga, M. E. (2011). Taphonomic and early diagenetic effects on the C and N stable isotope composition of  
299 cladoceran remains: implications for paleoecological studies, *Journal Of Paleolimnology*, 46(2), 203–213.  
300 <https://doi.org/10.1007/s10933-011-9532-y>.
- 301 Perga, M. E., Maberly, S. C., Jenny, J. P., Alric, B., Pignol, C., & Naffrechoux, E. (2016). A century of human-  
302 driven changes in the carbon dioxide concentration of lakes, *Global Biogeochemical Cycles*, 30, 93–104.  
303 <https://doi.org/10.1002/2015GB005286>.
- 304 Sage, R. F. (2001). Environmental and evolutionary preconditions for the origin and diversification of the C<sub>4</sub>  
305 photosynthetic syndrome, *Plant Biology*, 3(3), 202–213. <https://doi.org/10.1055/s-2001-15206>.
- 306 Schindler, D. E. (1997). Influence of food web structure on carbon exchange between lakes and the atmosphere,  
307 *Science*, 277(5323), 248–251. <https://doi.org/10.1126/science.277.5323.248>.
- 308 Shakun, J. D., Clark, P. U., He, F., Marcott, S. A., Mix, A. C., Liu, Z. Y., et al. (2012). Global warming preceded by  
309 increasing carbon dioxide concentrations during the last deglaciation, *Nature*, 484, 49–55.  
310 <https://doi.org/10.1038/nature10915>.
- 311 Sharkey, T. D., & Berry, J. A. (1985). Carbon isotope fractionation of algae as influenced by an inducible CO<sub>2</sub>  
312 concentrating mechanism, in *Inorganic Carbon Uptake by Aquatic Photosynthetic Organisms*, edited by Lucas, W.  
313 J. & Berry, J. A., p. 389–401, American Society of Plant Physiologists.
- 314 Smith, H. J., Fischer, H., Wahlen, M., Mastroianni, D., & Deck, B. (1999). Dual modes of the carbon cycle since the  
315 Last Glacial Maximum, *Nature*, 400, 248–250. <https://doi.org/10.1038/22291>.
- 316 Smyntek, P. M., Maberly, S. C., & Grey, J. (2012). Dissolved carbon dioxide concentration controls baseline stable  
317 carbon isotope signatures of a lake food web, *Limnology and Oceanography*, 57(5), 1292–1302.  
318 <https://doi.org/10.4319/lo.2012.57.5.129E>.
- 319 Sobek, S., Algesten, G., Bergstrom, A. K., Jansson, M., & Tranvik, L. J. (2003). The catchment and climate  
320 regulation of pCO<sub>2</sub> in boreal lakes, *Global Change Biology*, 9, 630–641. <https://doi.org/10.1046/j.1365-2486.2003.00619.x>.
- 322 Street-Perrott, F. A., Huang, Y., Perrott, R. A., Geoffrey, E., Philip, B., Ben, K. L., et al. (1997). Impact of lower  
323 atmospheric carbon dioxide on tropical mountain ecosystems, *Science*, 278, 1422–1426.  
324 <https://doi.org/10.1126/science.278.5342.1422>.
- 325 Stumm, W., & Morgan, J. J. (1995). *Aquatic chemistry: Chemical equilibria and rates in natural waters*, Wiley-  
326 Interscience, New York, USA.
- 327 Tanentzap, A. J., Kielstra, B. W., Wilkinson, G. M., Berggren, M., Craig, N., der Giorgio, P. A., et al. (2017).  
328 Terrestrial support of lake food webs: Synthesis reveals controls over cross-ecosystem resource use, *Science*  
329 *Advances*, 3(3), 1–10. <https://doi.org/10.1126/sciadv.1601765>.

- 330 Tranvik, L. J., Downing, J. A., Cotner, J. B., Loiselle, S. A., Striegl, R., Ballatore, T. J., et al. (2009). Lakes and  
331 reservoirs as regulators of carbon cycling and climate, *Limnology and Oceanography*, 54(6, part 2), 2298–2314.  
332 [https://doi.org/10.4319/lo.2009.54.6\\_part\\_2.2298](https://doi.org/10.4319/lo.2009.54.6_part_2.2298).
- 333 Wang, Q., Yang, X. D., Anderson, N. J., Zhang, E. L., & Li, Y. L. (2014). Diatom response to climate forcing of a  
334 deep, alpine lake (Lugu Hu, Yunnan, SW China) during the Last Glacial Maximum and its implications for  
335 understanding regional monsoon variability, *Quaternary Science Reviews*, 86, 1–12.  
336 <https://doi.org/10.1016/j.quascirev.2013.12.024>.
- 337 Wang, Y. J., Cheng, H., Edwards, L. R., An, Z. S., Wu, J. Y., Shen, C.-C., et al. (2001). A high-resolution absolute-  
338 dated Late Pleistocene monsoon record from Hulu Cave, China, *Science*, 294, 2345–2348.
- 339 Wang, Y. J., Cheng, H., Edwards, R. L., He, Y. Q., Kong, X. G., An, Z. S., et al. (2005). The Holocene Asian  
340 monsoon: links to solar changes and North Atlantic climate, *Science*, 308(5723), 854–857.  
341 <https://doi.org/10.1126/science.1106296>.
- 342