

1 Imprints of the Little Ice Age and the severe earthquake of 2001 on the aquatic ecosystem of a  
2 tropical maar lake in El Salvador

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32

## 33 **Abstract**

34 Using a 530-year sediment record from the maar Lake Apastepeque, El Salvador, and based  
35 on diverse geochemical and biological (cladocerans, chironomids, diatoms, ostracods, testate  
36 amoebae) indicators, we estimated climatic and environmental alterations during the Little Ice  
37 Age (LIA) and reconstructed the recent history of the lake. Results demonstrate relatively  
38 humid conditions in the mid-elevations (500 m a.s.l.) of El Salvador during most parts of the  
39 LIA, resulting in high lake levels. Contrarily, the first part of the LIA was characterized by  
40 drier climates comparable to studies from Mexico and Belize, which correlated this phase  
41 with the Spörer minimum. Regional comparison with palaeorecords from the northern  
42 Neotropics reveals a high heterogeneity in local expressions of the LIA in Central America,  
43 likely connected to the high topographic heterogeneity of the region. Since the beginning of  
44 the 20<sup>th</sup> century, Lake Apastepeque has experienced enhanced human impact expressed as  
45 increased nutrient supply. The most recent period was characterized by significant  
46 environmental disturbance, which we relate to an upper-crustal earthquake, one of the  
47 strongest over the last 500 years, that affected the region on 13<sup>th</sup> February 2001 (Mw=6.6,  
48 epicentre at 10 km depth, 30 km from the lake). The release of toxic bottom components such  
49 as hydrogen sulphide and high turbidity and turbulence of water caused major species  
50 turnover in the lake ecosystem, resulting in a massive fish kill and colonization by large  
51 cladocerans. Modern sediments still show slightly altered biota communities compared to pre-  
52 earthquake assemblages, indicating that the ecosystem has still not fully recovered.

53 **Key words:** Lake Apastepeque, 13<sup>th</sup> February 2001 earthquake, Central America, aquatic  
54 biota, palaeolimnology, geochemistry

## 55 **1. Introduction**

56 Tropical ecosystems of Central America are complex and characterized by high biological  
57 diversity and intricate ecological interactions such as food web energy transfer and primary  
58 productivity processes (Dirzo and Bonilla, 2013). These ecosystems are controlled by  
59 processes including climatic fluctuations, and marine intrusions, as well as volcanism and  
60 tectonic activities (Caballero and Ortega Guerrero, 1998; Slate et al., 2013; Pérez et al., 2021).  
61 The last two millennia have been marked by significant climatic variability, manifested by  
62 alternating wet and dry periods (Curtis et al., 1996; Dull, 2004a, b; Rodríguez-Ramírez et al.,

63 2015). Furthermore, this period is characterized by major environmental transformations  
64 caused by human activities such as deforestation and intensified agriculture, including  
65 widespread pasture and croplands. Consequences of these anthropogenic changes are loss of  
66 biodiversity, enhanced surface erosion, a higher influx of nutrients into fresh surface waters,  
67 resulting in a widespread deterioration of fresh water quality (Franco-Gaviria et al., 2018a,  
68 2020).

69 One of the most recent and prominent climate oscillations, which significantly altered  
70 ecosystems worldwide, was a cool interval known as the Little Ice Age (LIA). This event  
71 occurred approximately between 1300–1850 AD, with the coldest temperatures observed in  
72 the Northern Hemisphere during the interval of 1400–1700 AD. The LIA is assumed to have  
73 been triggered by solar forcing (Mann et al., 2009) and global intensification of volcanic  
74 activity (Crowley et al., 2008). Most of the available palaeoclimate reconstructions suggest  
75 that during the LIA, global temperatures decreased by 0.5–1.5 °C (Mann et al., 1998), but  
76 with great regional variability (Crowley et al., 2008). Conditions were particularly severe  
77 during two solar minima, known as Spörer (~1460–1550 AD) and Maunder (~1645–1715  
78 AD) (Eddy, 1976a, b). In the Caribbean region, coral data indicate an even higher magnitude  
79 of cooling, with temperatures 2–3°C lower than those of today (Winter et al., 2000).

80 The effects of the LIA on inland tropical ecosystems of Central America have been  
81 mainly investigated in Mexico (the Nearctic-Neotropical transition zone) (Lozano-García et  
82 al., 2007; Cuna et al., 2014) and Guatemala (Rosenmeier et al., 2002; Pérez et al., 2010; Vélez  
83 et al., 2011) but other regions of Central America remain poorly examined (Tsukada and  
84 Deevey, 1967; Dull, 2004a, b; Harvey et al., 2019). Conclusions from LIA research carried  
85 out in Guatemala and Mexico, however, are not unequivocal and consistent. Some findings  
86 point to a drier climate and a drop in lake level (e.g., Lake Luna in Mexico, Cuna et al. 2014),  
87 whereas analysis of a sediment core from Lake Verde (Mexico) provided evidence for humid  
88 conditions (Lozano-García et al., 2007). The palaeolimnological record of Lake Llano del  
89 Espino in El Salvador also revealed higher water levels during the LIA, albeit not linked to  
90 climate variability. The authors assumed that these changes were rather induced by  
91 subsidence of the lake basin, rejecting the hypothesis for wetter conditions during the LIA  
92 (Dull, 2004a).

93 Palaeolimnological studies on climate and environmental changes in Central America  
94 remain scarce. Therefore, to better understand the global expression of climate change, and its

95 effects on biota, especially in ecologically sensitive and diverse regions like the Neotropics,  
96 additional in-depth studies are needed. This gap in knowledge was the main motivation to  
97 undertake research in El Salvador. The study site is located in the middle of Central America  
98 and thus represents an ideal location for palaeoclimate research given its geographical  
99 position between the Pacific Ocean and the Caribbean Sea, heterogeneity of regional  
100 environments (0–2730 m a.s.l.), and continuous historical influence of pre-Hispanic cultures.  
101 An additional advantage of the chosen study site is its mid-elevation location, as most of the  
102 palaeoclimate reconstructions in the northern Neotropics come from the lowlands.

103         Pioneering work conducted in El Salvador, spanning the period from the early (Dull,  
104 2004a, b) to late Holocene (Tsukada and Deevey, 1967), used palynology and stable isotope  
105 analysis of bulk sediment to track the history of tropical savanna, changes in vegetation as a  
106 result of human activities, and revealed the beginning of maize agriculture (Tsukada and  
107 Deevey, 1967; Dull, 2004a, b). Anthropogenic effects on the environment of El Salvador have  
108 been mainly characterized by a reduction of forest cover, expansion of agriculture and lake  
109 eutrophication (Dull, 2004a, 2007). Human-induced alteration of ecosystems was initially  
110 caused by land use practices of ancient cultures. First evidence of agricultural cultivation  
111 occurred ~ 5000 cal yr BP and is shown by a rise in the abundance of weed pollen taxa in the  
112 sediment record from Lake Verde. Subsequently, high anthropogenic pressure on the local  
113 vegetation persisted, first interrupted by the eruption of Volcán Ilopango in 1520 cal yr BP  
114 (Dull, 2004b, 2007), which resulted in a human population decline for around 200 years. A  
115 second period of decreasing human impact in El Salvador was related to the depopulation of  
116 Central America in the 16<sup>th</sup> and 17<sup>th</sup> centuries due to deadly epidemics (Dull, 2007, et al.  
117 2010). The environmental consequence of this was a decrease in fire activity that allowed an  
118 increase in abundance of some tree and shrub taxa and forest regeneration (Dull, 2004a). This  
119 period of human population decline also coincided with the LIA. Forest expansion was again  
120 disturbed in the 19<sup>th</sup> century by a gradual recovery of the indigenous population (Dull, 2007)  
121 and a significant environmental transformation during the last centuries has been associated  
122 with demographic pressure and expansion of commercial cultivation (Dull, 2004a, b).

123         Despite the comprehensive studies carried out by Dull in El Salvador (2004a, b, 2007,  
124 et al. 2010) many questions remain. The vegetation history of El Salvador is well  
125 documented, but more detailed information on late Holocene climate evolution, especially  
126 regarding smaller-scale variations, and its effect on aquatic biota communities are lacking.

127 Moreover, considering the accelerating rates of human disturbance on both terrestrial and  
128 aquatic ecosystems (Dull, 2004a, b; Bhattacharya and Byrne, 2016), palaeoecological studies  
129 can help in tracking organism responses to different natural and anthropogenic pressures,  
130 allowing cause-effect relationships to be better understood and restoration measures to be  
131 implemented.

132 In this study, we investigated a continuous sediment record from the tropical maar  
133 Lake Apastepeque spanning the last ~ 530 years. By comparing biological proxies (such as  
134 cladocerans, chironomids, diatoms, ostracods, and testate amoebae) with geochemical  
135 proxies, we aim to track the effects of recent climate oscillations (e.g. the LIA), human impact  
136 and geological events (e.g. severe earthquakes) on the lake ecosystem. We especially sought  
137 to answer the following questions: 1) what was the effect of late Holocene climatic variability  
138 and anthropogenic activity on the environmental conditions and aquatic organisms of Lake  
139 Apastepeque? 2) what was the character of the LIA in the mid-elevations of El Salvador?, and  
140 3) how do climatic fluctuations in El Salvador correspond to the broader pattern recorded in  
141 Central America and circum-Caribbean regions? This knowledge will provide an essential  
142 base-line against which to evaluate future local climate change impacts more precisely.

143

## 144 **2. Regional setting and site location**

145 Central America is climatically sensitive due to its location within the convergence zone of  
146 northern and southern hemisphere trade winds, especially due to the confluence of air masses  
147 from the Atlantic and Pacific Oceans (Stansell et al., 2013). The main drivers of Central  
148 America's climate are the Intertropical Convergence Zone (ITCZ) (Diaz et al., 2001), the  
149 North Atlantic Oscillation (NAO) (Giannini et al., 2000) and the El Niño Southern Oscillation  
150 (ENSO) (Diaz et al., 2001). Changes in these systems have resulted in great climatic  
151 variability during the Holocene which were manifested as wet/dry cycles on centennial- to  
152 millennial-scales (Curtis et al., 1996).

153 The most variable climatic element in the region is rainfall, which is mainly controlled  
154 by the position of the ITCZ. Shifts of the ITCZ result in the annual bimodal cycle of  
155 precipitation, characteristic of the region (Karmalkar et al., 2011). Peak rainfall occurs  
156 between May and October, when the ITCZ reaches its northernmost position. Average annual  
157 precipitation varies between 1700–1900 mm (values for the period 1971–2001), while real  
158 average annual evapotranspiration equals 1000–1100 mm (UNESCO, 2006). Great

159 differences in topographic relief also result in significant variations in rainfall and temperature  
160 at the regional scale (Karmalkar et al., 2011). El Salvador is characterized by a high humidity  
161 of 70% and 84% during dry and wet seasons, respectively. The annual temperature oscillation  
162 is small with a mean ranging between 22–28°C (UNESCO, 2006). The maximum temperature  
163 is observed in April while the coldest months are December and January.

164 The study site is located close to the city of Apastepeque in the department of San  
165 Vicente in El Salvador, ca. 40 km west of San Salvador city (Fig.1). This region is  
166 characterized by the young volcanic landscape of San Vicente, where cinder cones, lava  
167 domes, crater lakes, and maars are common. In one of the craters Lake Apastepeque, a small,  
168 circular, and deep maar lake (ca. 0.35 km<sup>2</sup>, 54 m deep, 504 m a.s.l.) is located. The lake has  
169 steep walls, is surrounded by basaltic ash and angular blocks of andesite (Global Volcanism  
170 Program, 2013). The lake is situated within the Apastepeque Volcanic Field from which a  
171 fault-zone extends towards the east, and which is characterized by a semicircular scarp (Fig.  
172 S1). In general, El Salvador is a seismically highly active region due to the neighbouring  
173 Middle-America subduction zone. During the last 100 years, the country did experience  
174 several major earthquakes with a magnitude over 6.

175 The catchment of Lake Apastepeque (2.06 km<sup>2</sup>) consists of extensive croplands (Arino  
176 et al., 2012) sustained by fertile soils with high porosity (Flores and Miranda, 1999). In 2004,  
177 floating microalgae were recorded in the lake, indicating atypical water conditions likely due  
178 to nutrient run-off or enhanced weathering (Jiménez et al., 2004). Lake Apastepeque is mainly  
179 fed by precipitation; however, it is also connected to a groundwater aquifer, which drains to  
180 Río Ismateco (Flores and Miranda, 1999). Until recently, changes in precipitation/evaporation  
181 balance, and likely in groundwater level, led to lake level variations (> 1 m) throughout the  
182 year, causing a fluctuation in lake area from around 0.35 up to 1.6 km<sup>2</sup> towards the end of the  
183 rainy season (Jiménez et al., 2004; Climapesca, 2017). Recently, however, a report of the  
184 Ministry of Environment and Natural Resources of El Salvador (MARN, 2018) mentioned  
185 changes in the surface area of shallow Lake Ciega, located only 400 m south-east from Lake  
186 Apastepeque (Fig. S1). During the rainy season, Lake Ciega doubles its size, flooding  
187 agricultural and livestock lands. Therefore, we cannot exclude the possibility that, in the past,  
188 these two lakes have merged during the wet season. This is inspired by the assumption that  
189 Lake Ciega is the remnant of a larger lake (MARN, 2018).

### 190 **3. Materials and methods**

191 In autumn 2013, a 34 cm long sediment core APA 1.2. was retrieved from 47 m water depth  
192 from Lake Apastepeque, using an UWITEC gravity corer. In addition, water transparency and  
193 the maximum lake depth were measured *in situ* with a Secchi disk and a portable depth  
194 sounder, respectively. A WTW multi set 350i multiparametric probe was used to determine  
195 conductivity, dissolved oxygen, pH, and temperature. Water samples from 50 cm depth were  
196 collected for anion and cation analysis.  $\text{PO}_4^{3-}$ ,  $\text{NO}_3^-$ , and  $\text{SiO}_2$  were determined using  
197 spectrophotometric techniques immediately after field work. Cation concentrations were  
198 measured by an atomic absorption spectrophotometer, while  $\text{HCO}_3^-$  and  $\text{Cl}^-$  were determined  
199 by titration and potentiometric methods, respectively. Additionally, surface sediments were  
200 collected using an Ekman grab (the top 1 cm of sediments were taken assuming that these  
201 represent more recent conditions than the top 2 cm of the core) from the littoral zone (2.5 m)  
202 and from 47 m water depth for X-ray diffraction, cladoceran and diatom analyses. These two  
203 groups of organisms were selected for additional surface sediment analysis because they were  
204 the most abundant and best-preserved zoo- and phytoplankton, and because they are key  
205 components of the lake food web.

206

### 207 *3.1. Lithological description*

208 The sediment core APA 1.2 was transported to the laboratory and stored in cool conditions.  
209 The core was then cut in half length-wise and the sediment profile photographed, described  
210 (colour, texture). One half of the core was used for dating, whereas the other was sub-sampled  
211 at 2 cm-intervals for multiproxy analysis.

212

### 213 *3.2. Geochronology*

214 The core chronology was established using radionuclide and radiocarbon dating. Dried  
215 sediment samples were analysed for  $^{210}\text{Pb}$ ,  $^{226}\text{Ra}$ , and  $^{137}\text{Cs}$  by direct gamma assay in the  
216 Environmental Radiometric Facility at University College London, using an ORTEC HPGe  
217 GWL series well-type coaxial low-background intrinsic germanium detector.  $^{210}\text{Pb}$  was  
218 determined via its gamma emissions at 46.5keV, and  $^{226}\text{Ra}$  by the 295keV and 352keV  
219 gamma rays emitted by its daughter isotope  $^{214}\text{Pb}$  following three weeks storage in sealed  
220 containers to allow radioactive equilibration.  $^{137}\text{Cs}$  was measured by their emissions at  
221 662keV (Appleby et al., 1986). The absolute efficiencies of the detector were determined  
222 using calibrated sources and sediment samples of known activity. Corrections were made for

223 the effect of self-absorption of low energy gamma rays within the sample (Appleby et al.,  
224 1992).  $^{210}\text{Pb}$  activities were calculated by subtracting  $^{226}\text{Ra}$  activity (as supported  $^{210}\text{Pb}$ ) from  
225 total  $^{210}\text{Pb}$  activity. The use of the CIC (constant initial concentration) model was precluded  
226 by the non-monotonic variation in unsupported  $^{210}\text{Pb}$  activities.  $^{210}\text{Pb}$  chronologies were  
227 calculated using the CRS (constant rate of  $^{210}\text{Pb}$  supply) dating model (Appleby, 2001).  
228 Radiocarbon dating of extracted pollen by accelerator mass spectrometry (AMS) was  
229 performed for the bottom layer (34–32 cm) in a commercial laboratory (Beta Analytic). The  
230  $^{14}\text{C}$  date was calibrated using the curve IntCal20 (Reimer et al., 2020). The pollen extract was  
231 prepared from fresh sediments (ca. 4 g) according to the standard method (Berglund and  
232 Ralska-Jasiewiczowa, 1986).

### 233 *3.3. Elemental composition and geochemical proxies*

234 The bulk sediment elemental composition was measured on the upper 30 cm of the sequence  
235 at 2-cm resolution to determine total carbon (TC), total inorganic carbon (TIC), total organic  
236 carbon (TOC), and total nitrogen (TN). TC and TN were determined by an elemental analyser  
237 (LECO TruSpec CHN Macro). The C/N molar ratios were calculated from TC and TN. For  
238 the determination of the TIC content,  $\text{CO}_2$  was evolved during hot ( $70^\circ\text{C}$ ) phosphoric acid  
239 ( $\text{H}_3\text{PO}_4$ ) treatment and quantified conductometrically. The TOC content was calculated by  
240 subtraction of TIC from TC. Organic matter and carbonate content as well as the residual  
241 (total mass minus  $\text{CaCO}_3$  and organic matter) were determined by thermogravimetric loss-on-  
242 ignition (LOI) analyses with ignition at  $550^\circ\text{C}$  and  $950^\circ\text{C}$ , respectively (Heiri et al., 2001).

243 Concentrations of  $\text{PO}_4$ , S, Ca, Mg, Fe, Mn, and Ti were measured by ICP-OES  
244 spectrometer (Perkin Elmer Optima 2100 DV) according to DIN EN 13346 (Anonymous,  
245 2001). The pre-treatment of sediments included sieving (2 mm sieve) and separating into two  
246 fractions ( $< 2\text{mm}$  to  $\geq 63\ \mu\text{m}$ , and  $< 63\ \mu\text{m}$ ). Subsequently, samples were dried, weighed,  
247 ground into powder, and measured.

248 A portable energy-dispersive X-ray fluorescence spectrometer (EDXRF) (Analyticon  
249 NITON XL3t) was utilized to analyse concentration of K, Zr, Si, Ti, and Al. Each sample (~4  
250 g) was dried at  $55^\circ\text{C}$ , homogenized and ground into powder. Thereafter, sediments were  
251 transferred into plastic cups and covered with a mylar foil, placed on the EDXRF, and  
252 analysed for 120 s. The calibration was conducted using the certified reference material  
253 (CRM): GBW07312 (stream sediment), LKSD-2 and LKSD-4 (lake sediments; Lynch, 1990).



254 PO<sub>4</sub> and S were determined to follow changes in lake productivity (Boyle, 2001), while  
255 elemental concentrations of Ca, Mg, K, Si, Al, Ti, and Zr were measured in order to infer  
256 detrital influx (Rothwell and Croudace, 2015). Furthermore, K/Zr and K/Ti ratios were  
257 calculated to estimate grain-size variability throughout the core (Chawchai et al., 2016;  
258 Křibek et al., 2017). Results of Fe and Mn measurements, expressed as their molar ratio  
259 (Fe/Mn), were used to assess changes in redox conditions (Boyle, 2001).

260 Spearman correlation analysis was used to identify correlations among geochemical  
261 and lithological parameters. Statistical analysis on the z-scored data was run using R software  
262 (R Core Team, 2020) and significance of correlation was assessed at  $p < 0.05$ .

263 To identify the mineralogical composition of littoral and profundal sediments, powder  
264 X-ray diffraction analysis (PXRD) was used. Sediment samples were ground into powder and  
265 then analysed using a Bruker AXS D8 Advance X-Ray Diffractometer. The PXRD results  
266 were evaluated using the EVALUATION software (EVA) of Bruker.

### 267 *3.4. Biological proxies*

268 For the analyses of biological proxies, the sediment sequence was sampled at 2 cm intervals  
269 and further divided into subsamples for each proxy.

270 Cladocera analysis was carried out following Frey's method (Frey, 1986). Two cm<sup>3</sup> of  
271 wet sediment were heated in KOH solution (10%) to remove organic matter. The residue on a  
272 38 µm mesh sieve was backwashed and used as the sample with the volume brought up to 5  
273 mL with distilled water. The samples were then dyed with safranine. Three to four slides (0.1  
274 cm<sup>3</sup> each) were analysed for each sample at 100x, 200x and 400x magnification.  
275 Identification was made following Wojewódka et al. (2020a, b). The most common  
276 cladoceran remains, such as head shield, shell, postabdomen were identified, and at least 70  
277 individuals were counted for each sample (Kurek et al., 2010). The cladoceran abundance was  
278 expressed as a percentage of the sum of total individuals counted.

279 The procedure for diatom analysis was adapted from a standard method (Battarbee et  
280 al., 2001): 0.4 g wet sediment was treated with 37% HCl and 30% H<sub>2</sub>O<sub>2</sub> and heated at 70 °C  
281 to remove carbonates and to oxidize organic matter, respectively. Samples were washed with  
282 distilled water during preparation to dilute remnants of peroxide and acids. Naphrax® was  
283 used as a mounting medium to make permanent slides for light microscope (LM) analyses.  
284 Slides were analysed using a Leica DM 5000 B LM with Differential Interference Contrast

285 under oil immersion at  $\times 1000$  magnification. A minimum of 400 valves was counted in each  
286 sample. Diatom concentration was determined according to Battarbee and Kneen (1982) and  
287 identification was based on standard identification literature together with relevant taxonomic  
288 publications (e.g., Hofmann et al., 2011; Krahn et al., 2018, 2021). Species relative  
289 abundances were expressed as percentages of the total diatom individuals counted.

290 For chironomid analysis, 3 g of sediment were deflocculated in warm KOH solution  
291 (10%) for 20 min and then backwashed on a 90  $\mu\text{m}$  sieve (Walker and Paterson, 1985).  
292 Chironomid head capsules were hand-picked and permanently mounted in Berlese mounting  
293 medium. All head capsules were picked from each sample, ranging from 21 to 103  
294 individuals. Taxonomic identification was performed under a compound microscope at up to  
295 400x magnification, with reference to Hamerlík and Silva (2020). Species abundances were  
296 expressed as percentages of the sum of total remains counted.

297 For testate amoeba analysis, 1  $\text{cm}^3$  of sediments was backwashed on a sieve with 63  
298  $\mu\text{m}$  mesh. The resulting fraction was then analysed under a ZEISS Stemi 508  
299 stereomicroscope, and tests were extracted using a fine brush (Ellison and Ogden, 1987).  
300 Taxonomic identification was made using an optical microscope and a Scanning Electron  
301 Microscope, following relevant literature such as Kumar and Dalby (1998), and Sigala et al.  
302 (2015). Results were expressed as the number of individual tests per 1  $\text{cm}^3$ .

303 Three grams of wet sediments were used for ostracod analysis. Sediments were  
304 initially disaggregated with a solution of 3%  $\text{H}_2\text{O}_2$  for 12 hrs and then flushed with distilled  
305 water and sieved through 63  $\mu\text{m}$  mesh sieves. Ostracods were picked using a  
306 stereomicroscope and adult and juvenile valves were counted. Valves were stored in  
307 micropalaeontological slides. Species identification was conducted in valves of adult  
308 specimens only and following available literature (Pérez et al., 2013; Cohuo et al., 2017).  
309 Results were expressed as the number of specimens per 1 g of dry sediment.

310 Due to a high variation in sedimentation rate throughout the core, the total abundances  
311 of aquatic biota were expressed as fluxed, i.e., as number of individuals per  $\text{cm}^2\text{yr}^{-1}$ . Data  
312 were plotted with C2 version 1.7.7. (Juggins, 2007).

313

## 314 **4. Results**

### 315 *4.1. Lake Apastepeque limnological conditions*

316 In 2013, the water of Lake Apastepeque was alkaline (pH=8.6) with a low conductivity (ca.  
317 100  $\mu\text{S cm}^{-1}$ ).  $\text{HCO}_3^-$  was the dominant anion, followed by  $\text{Cl}^-$ . The dominant cations were  
318  $\text{Ca}^+$  and  $\text{Mg}^+$ . Moreover, a high concentration of  $\text{SiO}_2$  (ca. 28  $\text{mg L}^{-1}$ ) (Table S1) was  
319 observed in the lake water. Water transparency was ca. 6 m, and the lake had a low content of  
320  $\text{PO}_4^{3-}$  ( $<0.01 \text{ mg L}^{-1}$ ) and  $\text{NO}_3^-$  ( $0.4 \text{ mg L}^{-1}$ ).

#### 321 4.2. Core chronology

322 Total  $^{210}\text{Pb}$  activities reach equilibrium with the supported  $^{210}\text{Pb}$  at a depth of ca. 15 cm in the  
323 core. There is a decline in unsupported  $^{210}\text{Pb}$  activities in the top 6 cm, and little net decline  
324 from 6 to 14 cm (Fig. S2), suggesting changes in sedimentation rates.  $^{137}\text{Cs}$  was detected from  
325 2 to 15.5 cm. The  $^{137}\text{Cs}$  activity versus depth shows a peak at 6.3 cm (Fig. S2), but as the  
326 activities were low, confidence of using the peak for dating is not high. The low caesium  
327 activities put into question the real presence of the  $^{137}\text{Cs}$  peaks, and cause a mismatch between  
328 the peak in  $^{137}\text{Cs}$  and the  $^{210}\text{Pb}$  record. Therefore,  $^{137}\text{Cs}$  dating was excluded from further  
329 consideration.

330  $^{210}\text{Pb}$  chronologies were calculated using the CRS (constant rate of  $^{210}\text{Pb}$  supply)  
331 dating model (Appleby, 2001). Radiometric chronologies and accumulation rates of the  
332 sediments are given in Table S2 and shown in Figure S2a. Sediment core dating shows that  
333 the top 13.3 cm of the core covers approximately the last hundred years. Sedimentation rates  
334 show a slight increase from 13.3 to 8.3 cm (from 1910s until the 1950s) and peak at  $0.1 \text{ g cm}^{-2}$   
335  $\text{yr}^{-1}$  ( $0.272 \text{ cm yr}^{-1}$ ) at 8.3 cm. Sedimentation rate at 13–13.3 cm was lowest with  $0.0119 \text{ g cm}^{-2}$   
336  $\text{yr}^{-1}$  ( $0.028 \text{ cm yr}^{-1}$ ).

337 The lowermost sample (34–32 cm depth) was solely used for dating and yielded a  
338 conventional radiocarbon age of  $520\pm 30$  years BP based on extracted pollen. Calibration  
339 yielded an age of AD 1327–1349 (7.9 %) or AD 1395–1444 (87.5 %) with 95% probability  
340 (Table S3). The age of the sequence between 34 and 13.3 cm was interpolated by linear  
341 regression and using the date calculated by weighted average (AD 1413) for the bottom layer  
342 (34 cm). Results from both  $^{210}\text{Pb}$  and  $^{14}\text{C}$  were used to create the age-depth model (Fig. S3b).  
343 It should be stressed that interpolated age data are affected by errors resulting from  
344 assumptions about linear changes of sedimentation rate. Therefore, ages given for sediment  
345 layers between the bottom of the core and 13.3 cm below lake floor are approximated.

#### 346 4.3. Lithology and geochemical characteristics

347 The sediments are almost homogeneous with a fine-grained texture (clay) and dark brown  
348 colour. Sediments have a low carbonate content (<2%), while organic matter content varies  
349 from ca. 8 to 18 %. The vertical profiles of organic matter and carbonates display similar  
350 trends. The residual mineral matter content ranges from ca. 80 to 92% (Fig. S4) and mainly  
351 consists of fine-grained siliciclastic material. The alkaline metals (K, Ca, Mg) show inverse  
352 trends to TOC, PO<sub>4</sub>, organic matter and carbonate content. TOC varies slightly between 4.8–  
353 7%, while C/N ratio ranges between 13–15 throughout the core.

354 Correlation analysis displays two main groups of parameters positively correlated with  
355 each other at the p-value of 0.05 (Fig. S5). The first group encompasses alkaline metals (Ca,  
356 Mg, K), K/Ti, and K/Zr. Of these, Ca and Mg are strongly positively correlated (>0.75) with  
357 residual mineral matter and negatively with carbonates (< -0.75). The second group is  
358 composed of organic matter, carbonates, TOC, TN, PO<sub>4</sub>, S, and Fe. Elements from this group  
359 are moderately or strongly correlated (>0.5). Particular elements between these two groups,  
360 such as Ca, Mg, K (group 1) and TOC, TN, PO<sub>4</sub>, S (group 2), are negatively correlated (Fig.  
361 S5).

362 The highest sediment moisture (up to 80 %) is detected at the bottom of the core (30–  
363 24 cm), and corresponds to high contents of organic matter (up to 16 %), highest TOC and  
364 low carbonate content (1.4–1.5 %, Fig. S4). Between 30–24 cm, slightly lower ratios of C/N  
365 (13.3–13.6), higher TOC (6.3–7 %) and TN (0.5–0.6 %) are observed in comparison to the  
366 overlying sediment layer (24–14 cm). Furthermore, lower K/Zr (42–50) and K/Ti values (0.8–  
367 0.9) as well as high PO<sub>4</sub> value are documented. Lowest organic matter values (7.4–10.5) are  
368 recorded between 24–14 cm, coinciding with low values of carbonate (<1.4 %), PO<sub>4</sub> (up to  
369 0.19 %), and TOC (up to 6.2 %). Concentrations of alkaline metals such as K, Ca, Mg  
370 increase up to 0.6 %, 1.6 %, and 0.8%, respectively (Fig. S4). At the same time, the  
371 concentration of residual mineral matter in the sediments also rises. Zr and Si have their  
372 lowest contents in the layers between 24–18 cm. Sediments at the depths of 14–2 cm are  
373 characterized by gradually increasing concentrations of S, PO<sub>4</sub>, TOC, and carbonates along  
374 with gradually decreasing Ca, Mg, and K content. The uppermost part of the sediment core  
375 (2–0 cm) is marked by the highest content of organic matter (> 18%), S (0.52 %), high Fe/Mn  
376 (158) and lower values of K/Zr (50.7) and K/Ti ratio (0.9).

377 XRD analysis of littoral sediment samples includes the following mineral phases:  
378 plagioclase (likely andesine), montmorillonite, quartz, and amphibole (magnesiohornblende),

379 diopside, forsterite (Fig. S6). Profundal sediments are composed of plagioclase (likely  
380 andesine), montmorillonite (bentonite), halloysite, kaolinite, forsterite, quartz, diopside,  
381 microcline (Fig. S6). All of these phases are silicate minerals that include Ca and/or Mg, Na,  
382 Al, sometimes Fe, and K (microcline and halloysite).

#### 383 4.4. Changes in aquatic fauna and flora assemblages

##### 384 Cladocerans

385 Fifteen taxa of subfossil cladocerans were identified in the record and an additional five taxa  
386 were found in the surface sediment samples (Fig. S7). Planktonic taxa dominate through the  
387 entire sediment sequence. *Bosmina* is the dominant taxa of the Cladocera assemblage in the  
388 lowermost portion of the record (30–26 cm). From 26 to 2 cm, planktonic *Bosmina* sp. and  
389 *Liederobosmina* sp. predominate with 59% and 24% on average, respectively.

390 A decrease in Cladocera flux and a higher share of littoral taxa are noted between 26  
391 and 12 cm. In total, 11 taxa are present. Between 12 and 2 cm, cladoceran flux and number of  
392 species increases (up to 14 per sample). The uppermost layer (2–0 cm) is characterized by a  
393 completely different Cladocera species composition. Dominance shifts from Bosminidae to  
394 *Daphnia laevis*. *Liederobosmina* sp. (planktonic) totally disappears. In addition, a significant  
395 number of ephippia of planktonic *Moina* sp. is observed. In surface sediments (collected using  
396 Ekman grab; Fig. S7), Bosminidae reappear and the abundance of *Daphnia laevis*  
397 (planktonic) decreases sharply.

##### 398 Diatoms

399 In total, 104 different diatom taxa were observed. Twelve taxa show relative abundances of  
400 >3% in at least one sample (Fig. S8).

401 Sediment layers at the depth of 30–26 cm are characterized by planktonic taxa  
402 *Fragilaria salvadoriana* (~35.7%), *Fragilaria maarensis* (~21.5%), *Aulacoseira granulata*  
403 var. *granulata* (~8.6%), and *Aulacoseira granulata* var. *angustissima* (~7.6%). Benthic taxa  
404 constitute only around 19%. Diatom fluxes are low and stable with around  $4 \times 10^6$  valves  $\text{cm}^{-2}$   
405  $\text{yr}^{-1}$ . Furthermore, between 26–22 cm, an overall dominance (>80%) of *Achnanthydium*  
406 *neotropicum* and relatively high fluxes of diatoms (up to  $\sim 13 \times 10^6$  valves  $\text{cm}^{-2} \text{yr}^{-1}$ ) are  
407 recorded. From 22 to 20 cm we observe a short return to higher abundances of planktonic,  
408 needle-shaped *Fragilaria* sensu lato and *Aulacoseira* taxa (37.7%). However, *A. neotropicum*

409 still dominates this depth with 39%. Between 20 and 6 cm, assemblages are again dominated  
410 by *A. neotropicum* (80–86%). Diatom fluxes are generally low (mean  $\sim 4 \times 10^6$  valves  $\text{cm}^{-2} \text{yr}^{-1}$ ),  
411 but progressively increase towards the top (up to  $\sim 23 \times 10^6$  valves  $\text{cm}^{-2} \text{yr}^{-1}$ ). From 6 to 2  
412 cm, highest diatom fluxes are reported (up to  $69 \times 10^6$  valves  $\text{cm}^{-2} \text{yr}^{-1}$ ). The uppermost  
413 sediment layer (2–0 cm) is marked by a significant change in abundant taxa. The assemblage  
414 is again dominated by planktonic taxa (63.1%) out of which *A. granulata* var. *granulata*  
415 (55.4%) is by far the most dominant species, and the diatom flux drops to  $\sim 3 \times 10^6$  valves  $\text{cm}^{-2} \text{yr}^{-1}$ .  
416 In the surface sediments collected using Ekman grab the abundances of *A. neotropicum*  
417 increases again (42.9%). However, the appearance of several new taxa (e.g. *Achnanthydium*  
418 *straubianum*, *Achnanthydium* cf. *saprophilum*) and higher abundance of *Achnanthydium*  
419 *minutissimum* (9.6%) are observed as well.

#### 420 Chironomids

421 In total, 1004 chironomid remains were recorded, and 32 taxa were identified (Fig. S9).  
422 Subfamilies Tanypodinae (50% of total abundance) and Chironominae (49%) dominate  
423 through the sediment sequence. The most frequent taxa belong to predators, such as  
424 *Ablabesmyia* sp., *Labrundinia* type 2 and 3, and the detritus-feeder *Goeldichironomus* type 1,  
425 representing more than 90% of the overall abundance.

426 The lowermost portion of the sediment core (30–24 cm) is characterized by overall  
427 low diversity (maximum 13 taxa), with the prevalence of Tanypodinae and low proportion of  
428 Chironominae. Between 24 and 20 cm, taxon richness increases up to 21, and the proportion  
429 of the subfamily Tanypodinae to Chironominae decrease considerably. In the sediment layers  
430 between 20 and 10 cm, the proportion of Chironominae increases with *Goeldichironomus*  
431 becoming the predominant genus. From 10 to 2 cm, subfamily Tanypodinae reaches its lowest  
432 proportion, *Goeldichironomus* remains dominant. The top of the core (2–0 cm) is  
433 characterised by a sudden and short-lasting decrease in taxon richness, the increase of  
434 Tanypodinae morphotypes, and the dominance of *Labrundinia* type 3.  
435

#### 436 Testate amoebae

437 A total of seven morphotaxa of testate amoebae were identified. Amoeban abundance was  
438 generally low throughout the core, and only 88 individuals were found in the entire sediment  
439 sequence (Fig. S10). The highest abundances were recorded between 20–18 cm, 16–14 and 8–

440 4 cm (11–23 tests cm<sup>-3</sup>, 0–5 tests cm<sup>-2</sup> yr<sup>-1</sup>). The dominant species throughout the core is  
441 *Centropyxis aculeata*, while the rest of the taxa are rather rare (<5 tests cm<sup>-3</sup>). Only two  
442 centropyxid taxa (*Centropyxis aculeata*, *Centropyxis aculeata* “discooides”) are present in the  
443 bottom sediments (30–24 cm). Between 24 and 10 cm, several new taxa appear (*Arcella*  
444 *discooides*, *Arcella megastoma*, *Diffflugia oblong* strain a “oblonga”) but are low in abundance  
445 (3–1 tests cm<sup>-3</sup>). Sediment layers between 10–2 cm stand out by the constant presence of  
446 *Arcella discooides*. In the top of the core (2–0 cm) almost all taxa disappear, except for  
447 *Centropyxis aculeata*, and *Cyclopyxis kahli* appears for the first time.

448

449 Ostracods

450 The overall abundance of ostracods was low (38 individuals in total) (Fig. S10). Only  
451 *Keysercypria* sp. was identified. This is a nektobenthic species, characterized by well-  
452 developed swimming structures of antennae. It is highly abundant in the water column of the  
453 modern lake, and it seems to prefer deep waters. Ostracods were present only in the  
454 lowermost sediments between 30 and 26 cm and from 8 cm towards the top.

## 455 5. Discussion

456 5.1. Lake ecosystem responses to the Little Ice Age (zones I and II, 30 to 14 cm, 16<sup>th</sup> to 19<sup>th</sup>  
457 centuries)

458 The Little Ice Age (LIA) has been identified as a phase of fluctuating climatic conditions  
459 expressed by temperature decrease and changes in humidity due to an alteration of  
460 precipitation and evaporation (Winter et al. 2000, Hodell et al., 2005; Lozano-García et al.,  
461 2010; Cuna et al., 2014). The onset of the LIA in Mexico and Central America has mostly  
462 been dated from the beginning of the 15<sup>th</sup> century in the lowlands and middle elevation areas  
463 (Hodell et al., 2005; Lozano-García et al., 2010; Pérez et al., 2010; Rodríguez-Ramírez et al.,  
464 2015; Wu et al., 2016), although by 1360 AD, the effects of the LIA were already observed in  
465 high mountain areas of central Mexico (Cuna et al., 2014).

466 The LIA in the northern Neotropics is recognized as an environmental disruptor of  
467 ecological stability of aquatic systems, for example being associated with species turnovers  
468 recorded in lake sediments. This period was characterized by the presence of cold-water zoo-  
469 and phytoplankton species (Cuna et al., 2014). In Lake Apastepeque, LIA effects on the

470 biological community resulted in a relatively low diversity and frequent species turnovers  
471 (Fig. 2). Biota and geochemistry revealed three main hydroecological zones over the last 500  
472 years and one abrupt, geological event, likely related to the earthquake occurring on 13<sup>th</sup>  
473 February 2001 (GE I; Fig. 2). Our reconstruction reveals the heterogeneous character of the  
474 LIA, manifested mainly in water level changes which were reflected in aquatic biota  
475 assemblages. The basal sediments of the core (30 to 26 cm) represent the older part of the LIA  
476 (probably 16<sup>th</sup> century; Fig. 2). Based on biological and geochemical evidence, we infer that  
477 Lake Apastepeque was characterized by deep waters and moderate biological productivity  
478 during this time. Cladoceran and diatom assemblages were dominated by planktonic taxa,  
479 suggesting relatively deep-water conditions together with a rather weakly developed littoral  
480 zone. High water levels are also indicated by the presence of only few centropyxids in the  
481 testate amoebae assemblage, and the ostracod *Keysercypria* sp., which is well adapted (large  
482 swimming setae) to inhabit the water column. The low diversity and abundance of  
483 chironomids reflects limited habitat availability. The limited littoral zone is likely a result of  
484 the typical conical morphometry of maar type lakes. The presence of the cladoceran *Bosmina*  
485 sp. and the diatom *A. granulata* s.l. together with the prevalence of the chironomid genus  
486 *Labrundinia*, may indicate mesotrophic waters (Fig. 2) (Hamerlík et al., 2018). The relatively  
487 low share of *A. neotropicum*, a species that dominates through almost the entire sediment  
488 sequence, may suggest a different mixing behaviour of the lake or changes in water depth. *A.*  
489 *neotropicum* is a new species described from the sediment core of Lake Apastepeque,  
490 therefore, its ecological requirements are not well known yet. Although all species of  
491 *Achnantheidium*, except for *A. catenatum*, are considered benthic (Marquardt et al., 2017),  
492 Vázquez and Caballero (2013) observed high abundances of the species *A. minutissimum* in  
493 plankton samples of eastern Mexico. The authors suggest that this taxon possibly had an  
494 epiphytic habitat attached to floating algae, which flourished during times of increased water  
495 column stratification. However, lake level changes with expansion of the littoral zone  
496 favouring benthic habitats might also be a possibility. Therefore, we assume that the  
497 domination of *Fragilaria* species and low share of *A. neotropicum* may be the result of deep  
498 water conditions with limited benthic habitat and/or more frequent/pronounced turnover of  
499 epilimnion under drier conditions.

500 High concentration of TOC, TN, and PO<sub>4</sub> in the sediment also support relatively high  
501 trophic status. At the same time, the lower Fe/Mn ratio indicates more oxygenated conditions



502 in the epilimnion, probably due to increase volumetric ratio of epilimnion to hypolimnion  
503 (Townsend, 1999) and/or weaker stratification. On the other hand, the low number of  
504 ostracods and testate amoebae indicate unfavourable conditions for their development or their  
505 poor preservation (likely associated with anoxic conditions due to decomposition of organic  
506 matter in the deeper part of the water column). The species assemblage of testate amoebae  
507 suggests persistent stressful environmental conditions, related to deep water conditions,  
508 oxygen availability, limited vegetation and low organic matter content, throughout the whole  
509 time spanning the core (Charqueño et al., 2021).

510 Stable C/N ratios of 13–14 indicate a mixture of aquatic and terrestrial biomass  
511 (Meyers and Ishiwatari, 1993). The slightly lower C/N ratios recorded in this zone could have  
512 been caused by a lower input of terrigenous organic matter. Lower terrigenous fluxes are  
513 further supported by lower content of residual mineral matter. At the same time, low K/Zr  
514 ratios suggest coarser sediments (Křibek et al., 2017) than in the following period. In this  
515 case, however, low K/Zr ratios were likely caused by a lower input of clay sediments from the  
516 catchment, not by higher input of coarse particles (sand fraction). This is further supported by  
517 low variability in the content of both Ti and Zr throughout the record.

518 In the younger part of the LIA (probably between the beginning of 17<sup>th</sup> and the end of  
519 19<sup>th</sup> century, zone II), a marked decrease in total fauna and flora abundance in the sediment  
520 can be observed. The development of the littoral zone significantly changed the habitats of  
521 Lake Apastepeque during this period. Based on the responses of individual proxies, two  
522 different climatic scenarios and related changes of the littoral zone are proposed (Fig. 3): 1)  
523 relative expansion of the littoral zone by lake level drop due to precipitation decrease  
524 (Scenario 1) or, alternatively, 2) increasing lake level in a wetter environment due to lower  
525 evaporation and transport of biological remains from the littoral to profundal zone near to the  
526 coring site (Scenario 2). Increasing contribution of littoral cladocerans and benthic diatoms  
527 may have resulted from environmental changes caused by both Scenario 1 and 2 (Fig. 3).  
528 Concurrently, the chironomid record is marked by a relative increase of the subfamily  
529 Chironominae, especially of the genus *Goeldichironomus*, which mostly inhabits fine  
530 sediments in the profundal zone (supporting Scenario 2). However, this genus is ecologically  
531 versatile with some species also living on macrophytes (Scenario 1 and 2). Predominance of  
532 *Goeldichironomus* along with the presence of the testate amoeba *Arcella discoidea* (Sigala et  
533 al., 2018; Charqueño et al., 2020) suggests hypoxic conditions, at least temporarily (Fig. 2).

534 Furthermore, high water levels with more diluted waters (low carbonate content) could have  
535 created unfavourable conditions for ostracod development. The absence of ostracods in the  
536 sediments could have been also caused by poor preservation, or some combination of both  
537 high-water and low oxygen levels as well as poor preservation.

538         Considering that Lake Apastepeque is a maar lake, characterized by steep and almost  
539 vertical walls, surrounded by berms and low hills that rise sharply from the lakeshore, we  
540 assume that the presence of both benthic and littoral species resulted from a broadening of the  
541 littoral zone and an expansion of benthic habitats related to the increase of lake level from a  
542 wet environment (Fig. 3, Scenario 2). We assume that apart from the mixing and turbulence  
543 of the water column, the steep morphology of the maar lake led to efficient transportation of  
544 benthic biota remains from shallower areas to deeper sites.

545         Scenario 2 is further supported by geochemical indices which suggest increasing  
546 humidity in the area. As shown by the XRD results, modern Apastepeque sediments consist of  
547 minerals rich in alkaline metals, silica, and aluminium. Thus, a gradual increase of alkaline  
548 metals (Ca, Mg, K) and the K/Zr ratio suggest enhanced chemical weathering of soils and/or  
549 rocks in the catchment of Lake Apastepeque (basaltic ash and andesite are rich in Si, Al, K,  
550 Ca, Ti, Fe, Zr, Mg) under more humid conditions (Colman and Dethier, 1982), leading to  
551 higher input of clay minerals (weathering products). On the other hand, the lack of significant  
552 changes in Al and Si content may be explained by their lower rates of migration in dissolution  
553 processes, while alkaline metals are at the beginning of the element migration ranking (Lo et  
554 al., 2017). Consequently, strongly weathered rocks consist mainly of Si, Al, and Fe due to the  
555 previous leaching of bases (e.g., K, Ca, Mg and Na) from the crystalline structure.  
556 Subsequently, rather stable concentrations of Ti and Zr exclude significant changes in detrital  
557 input from mechanical weathering (Haug et al., 2001). Therefore, the higher input of alkaline  
558 metals suggests increased effective moisture, which in turn supports Scenario 2. This period,  
559 in all likelihood, was characterized by lower evaporation compared to the older part of the  
560 LIA (probably the period between the end of 15<sup>th</sup> to end of 16<sup>th</sup> centuries, zone I) and thus  
561 reduced water losses.

562         Subsequently, in the younger part of the LIA (probably the period between the  
563 beginning of 17<sup>th</sup> and the end of 19<sup>th</sup> century), the trophic state of Lake Apastepeque was  
564 lower than during the older part of the LIA. This period overlaps with the decimation in the  
565 indigenous population associated with the arrival of Spanish conquistadors, and, in turn,

566 decreasing human pressure. Forest regeneration, which occurred in El Salvador at that time,  
567 could have reduced watershed erosion, causing lower nutrient influx to surface freshwaters.  
568 Therefore, environmental change at that time in Lake Apastepeque presumably was induced  
569 by both a reduction in human activities and a climatic shift. In our record, the decrease in  
570 nutrient flux and trophic state is indicated by geochemical indices and the reduced abundance  
571 of biota. The same trends shown by carbonates, organic matter, TOC, sulphur, PO<sub>4</sub> and their  
572 positive correlation, underline the relationship of CaCO<sub>3</sub> precipitation with lake productivity.  
573 Increased productivity may cause a rise in biological consumption of CO<sub>2</sub>, and, in turn,  
574 precipitation of CaCO<sub>3</sub> (Boyle, 2001). The CaCO<sub>3</sub> record (determined by LOI), however, does  
575 not follow the TIC trend (determined by the elementary analyser) but this may result from the  
576 limitations of the LOI method (Santisteban et al., 2004) and therefore should be interpreted  
577 with caution. In spite of that, decreased trophic levels are indicated by lower TOC and PO<sub>4</sub>,  
578 and likely caused a reduction in flora abundance and lower biogenic removal of CO<sub>2</sub>, and, in  
579 turn, a decrease of CaCO<sub>3</sub> production (Boyle, 2001).

580 Our finding of higher lake levels during the LIA corresponds with Dull's (2004a)  
581 finding in the Laguna Llano del Espino (western El Salvador). He observed an increased  
582 contribution of *Potamogeton* sp. during the LIA which was interpreted as lake deepening.  
583 However, Dull (2004a) hypothesized that this was driven by subsidence, because he did not  
584 observe similar hydrological changes in two other lake records from El Salvador (Lake Verde  
585 and Lake Cuzcachapa; Dull, 2004a). It is possible that differences between Salvadorian lakes  
586 are due to their topographic settings and/or other abiotic factors at the local level. Laguna  
587 Verde is located ca. 1600 m a.s.l. within the Cordillera de Apaneca, while Lake Cuzcachapa  
588 and Laguna Llano del Espino are situated at mid-elevations (ca. 700 m a.s.l.). However, Lake  
589 Cuzcachapa is located at the lee side of the Cordillera de Apaneca, that, in turn, could have  
590 caused a rain shadow effect. Therefore, we hypothesize that mid-elevation lakes (500–1000 m  
591 a.s.l.; Echeverría Galindo et al., 2019) located in a more open landscape, such as Lake Llano  
592 del Espino and Lake Apastepeque, were under the influence of moist air masses. On the other  
593 hand, the region of Lake Cuzcachapa and Lake Verde today is characterized by higher  
594 precipitation and lower evaporation than the areas of Lakes Llano del Espino and  
595 Apastepeque (UNESCO, 2006). These differences emphasize the need to extend multi-proxy  
596 palaeolimnological research in El Salvador to improve our understanding of local climate  
597 dynamics.

598 It is also important to mention that during the younger part of the LIA, (ca. AD  
599 1700–1750, 22–20 cm depth) a marked shift in diatom assemblages from *A. neotropicum* to  
600 *Fragilaria* species occurred. This change likely indicates conditions similar to those recorded  
601 in the older part of the LIA, i.e. lower lake levels with limited littoral and benthic habitats  
602 and/or weaker stratification. Interestingly, the environmental turnover at that time was only  
603 reflected by the diatom record and may result from diatom sensitivity to changes in water  
604 depth and water column mixing (Vázquez and Caballero, 2013; Hofmann et al., 2020). As a  
605 result, diatoms may record these smaller-scale changes more accurately than other biological  
606 proxies, which respond less sensitively to small fluctuations of water level and water mixing.

607

## 608 *5.2. The Little Ice Age in Central America – a regional perspective*

609 A comparison of our results with previous studies in the northern Neotropical region (Mexico,  
610 Central America and the circum-Caribbean region) provides a wider context for climate  
611 variability during the LIA (Table S4, Fig. 4). The magnitude of cooling across the region  
612 varied spatially from ~ 1° C (Florida coast; Fig. 4 – no. 30; Lund and Curry, 2006) to ~2–3° C  
613 (Puerto Rico coast; Fig. 4 – no. 27; Winter et al., 2000; Nyberg et al., 2002). To date,  
614 quantitative temperature reconstructions from lake sediments, however, are scarce in Central  
615 America (Table S4, Fig. 4).

616 Two intervals (Spörer and Maunder minima) of colder conditions during the LIA (AD  
617 1300–1850) are usually recorded in the northern Neotropics. However, there are  
618 inconsistencies between different regional records regarding their intensity. Some records  
619 from Mexico, Puerto Rico and Panama indicate that the Spörer minimum was the coldest  
620 and/or driest period during the LIA (Nyberg et al., 2002; Rodríguez-Ramírez et al., 2015;  
621 Correa-Metrio et al., 2016) while others indicate the most severe conditions during the  
622 Maunder minimum (Black et al., 2007; Cuna et al., 2014). In Belize, according to stalagmite  
623 reconstruction, the LIA climate was relatively wet, with one short dry period at the end of the  
624 15<sup>th</sup> century (Webster et al., 2007). An similar scenario for the LIA has been determined using  
625 data from western Mexico (Rodríguez-Ramírez et al., 2015) that indicate relatively wet  
626 conditions persisting throughout most of the LIA with a short dry interval at the beginning  
627 and a slightly pronounced Maunder minimum. Such patterns seem to be similar to those  
628 suggested by the proxy data from Lake Apastepeque.

629 The most distinctive changes of the LIA in the northern Neotropics were associated  
630 with water balance (evaporation/precipitation ratio). However, the climate pattern during the  
631 LIA is less well recognized and seems to be inconsistent across Central America. Several  
632 studies signal a coherent response to climate during the LIA in Central America and the  
633 circum-Caribbean region, especially in the north, and display a shift towards drier conditions  
634 (Table S4, Fig. 4 – sites: 1, 2, 9; 13, 21, 22, 25, and 26). By contrast, there are several records  
635 where wet/or relatively wet conditions have been reported (Table S4, Fig. 4 – sites: 3, 4, 5, 6,  
636 7, 8, 10, 15, 16, 18, 19, 23, 24 and 28). In palaeoclimate records, especially from sites located  
637 in the middle of Central America, the LIA is documented as a period of increased moisture  
638 and lower evapotranspiration (Table S4, Fig. 4 – sites: 3, 4, 5, 6, 7, 10, 18, 23 and 24). Results  
639 of  $\delta^{18}\text{O}$  in speleothems located in the northwest Yucatán Peninsula also suggest relatively wet  
640 conditions (Fig. 4 – no. 10; Medina-Elizalde et al., 2010), especially between 1490–1580 AD  
641 and 1760–1828 AD. The observations mentioned above therefore seem to oppose other  
642 interpretations from the Yucatán Peninsula, where data suggest that the LIA was a period of  
643 dry conditions (Hodell et al., 2005). Alternatively, a reconstruction from mid elevation in  
644 Guatemala (Lake Amatitlán) demonstrates lower lake water levels prior to the LIA (875–1375  
645 AD), followed by increasing lake levels between 1375 and 1875 AD, and finally reduced  
646 water level again from 1875 AD to the present (Fig. 4 – no. 18; Vélez et al., 2011). These  
647 changes are opposite to the trend recorded in lowland Lake Petén Itzá, where relatively wet  
648 conditions were recorded, although with a trend towards drier conditions (Fig. 4 – no. 14;  
649 Pérez et al., 2010). These observations could suggest quite high moisture availability during  
650 the LIA. On the other hand, the isotopic data from the record of Lake Salpetén (Guatemala,  
651 near Lake Petén Itzá) point to rather dry conditions (Fig. 4 – no. 13; Rosenmeier et al., 2002).  
652 However, Pérez et al. (2010) interpreted a slight decrease in  $\delta^{18}\text{O}$  values in Lake Salpetén  
653 (Rosenmeier et al., 2002) as a higher water level, similar to Lake Petén Itzá. Moreover, Pérez  
654 et al. (2010) indicated that wet intervals (especially ca. ~1580 and ~1650 AD) could be  
655 caused by increased winter precipitation. A similar conclusion was drawn by Lozano-García  
656 et al. (2007) who assumed that a critical factor explaining LIA climates may be winter  
657 precipitation. It is noteworthy that records of wet conditions and/or lower evaporation come  
658 mainly from middle altitude (500–1000 m a.s.l.) or highland lakes located < 2500 m a.s.l., for  
659 example from Lake Santa Maria del Oro (Mexico), which is considered a suitable site for  
660 palaeoclimatic study due to its strong dependence on regional variables (Sigala et al., 2017).

661 Drier conditions during the LIA have been explained by a more southward  
662 displacement of the ITCZ (Haug et al., 2001; Hodell et al., 2005), probably caused by a rise in  
663 the meridional temperature gradient of the sea surface (Hodell et al., 2005). Cooler SSTs of  
664 the Atlantic correspond to a more southerly position of the ITCZ (Haug et al., 2001) which  
665 persisted until the onset of the 19<sup>th</sup> century (Lechleitner et al., 2017). Additionally, a more  
666 southern position of the ITCZ results in an enhancement of the north-easterly trade winds  
667 which, in turn, leads to a lower moisture content in the atmosphere and a reduction of  
668 precipitation (Nyberg et al., 2002). Additional factors controlling moisture availability in the  
669 region are the activity of the North Atlantic monsoon and El Niño or Pacific tropical storms  
670 (Metcalf et al., 2000; Stansell et al., 2013; Rodríguez-Ramírez et al., 2015). The LIA has  
671 been linked to a more negative phase of the NAO (Stansell et al., 2013), associated with the  
672 more southerly position of the ITCZ (Lechleitner et al., 2017) and high activity of El-Niño  
673 (Mann et al., 2009). In some regions, orography and fractional convergence may have caused  
674 increased rainfall despite a more southern position of the ITCZ (Hastenrath, 1976). However,  
675 any of the aforementioned mechanisms do not explain the discrepancies among Central  
676 American paleorecords.

677 The disparities between these independent records suggests that the mechanisms of  
678 climate forcing are much more complex, and archives of climatic change are strongly  
679 influenced by local hydrological balance and catchments. This region is characterized by high  
680 geographic and geomorphic variability which results in diverse ecological, tectonic,  
681 lithological, and climatic zones (Pérez et al., 2011). The complex and diverse topography  
682 results in considerable gradients in humidity, precipitation, and wind (Karmalkar et al., 2011).  
683 The climate is additionally complicated by the collision of two air masses from the Atlantic  
684 and Pacific Oceans. Geographical configurations, therefore, result in the region being  
685 characterized by a broad microclimate spectrum. The diversification of abiotic factors may be  
686 a reason for the heterogeneous response of ecosystems to global climate changes related to the  
687 LIA. Similar conclusions were drawn in a recently published paper by Obrist-Farner et al.  
688 (2022). They suggest that any single climatic factor (e.g., ITCZ, NAO, ENSO) cannot explain  
689 the full regional patterns of hydroclimatic changes in Central America and, therefore, the  
690 disparate signals derived from paleorecords are a result of a combination of several driving  
691 factors.

692 We would like to also highlight that most of the available palaeorecords are from  
693 lakes, which are very diverse in Central America with respect to their origin and other abiotic  
694 parameters (Pérez et al., 2011; Sigala et al., 2017). These lakes encompass shallow to deep  
695 waterbodies of different origin (volcanic, karstic, and tectonic) and morphometry, that are  
696 located from lowlands to highlands. The implication of such diversity could be their different  
697 sensitivities to local and regional variables (Sigala et al., 2017). For instance, karstic lowland  
698 waterbodies, like Lake Petén Itzá and Lake Salpetén, may be more sensitive to changes in  
699 evaporation and precipitation ratio (E/P), while shallow lowland lakes (e.g., Lake El Gancho)  
700 and shallower high mountain lakes (e.g., Lake La Luna and Lake El Sol) may display more  
701 pronounced drier period signals than deep lakes (e.g., Lake Aljojuca, Lake Petén Itzá).  
702 However, Obrist-Farner et al. (2022), further suggest that system diversity (including lakes),  
703 may not be the main source of discrepancy as they found disparities even when comparing  
704 similar systems or speleothem records from the same cave.

705 Considering the above, further work is required to resolve the character of the LIA in  
706 the studied region and to assess the role of local conditions on climate records in Central  
707 America.

### 708 *5.3. Post-Little Ice Age environmental conditions in Lake Apastepeque (zone III, 14–2 cm,* 709 *20<sup>th</sup> century)*

710 Modern environmental conditions were established with the end of the LIA.  
711 Historically, the 19<sup>th</sup> and 20<sup>th</sup> centuries coincide with recovery of the indigenous population  
712 that declined over 90% in the 16<sup>th</sup> and 17<sup>th</sup> centuries due to epidemics associated with the  
713 arrival of Spanish conquistadors (Dull, 2007, et al. 2010). This period of low human  
714 population was reflected in a decrease in anthropogenic pressure on the environment and, as a  
715 consequence, forest expansion (Dull, 2004b). Later, a gradual recovery of the El Salvador  
716 population and, in turn, an increase in related anthropogenic disturbance caused  
717 environmental transformation in the 19<sup>th</sup> and 20<sup>th</sup> centuries (Dull, 2007). Demographic  
718 pressure and extensive agriculture have led to deforestation, increasing erosion, and  
719 eutrophication in lakes (Dull, 2007).

720 In the sediment record of Lake Apastepeque, an enhanced nutrient flux is documented  
721 by abruptly increasing abundance of cladocerans, a higher share of *A. granulata* that is an  
722 indicator of eutrophication (Kilham et al., 1986), along with higher deposition ratio of lake

723 sediments and slightly higher TOC, TN, and PO<sub>4</sub> values since the beginning of the 20<sup>th</sup>  
724 century. Extension of croplands (Arino et al, 2012, Fig. S1) and agricultural activities in the  
725 catchment, especially developing sugar cane plantations (Díaz Ayala et al., 2004; Climapesca,  
726 2017) could have induced the trophic state increase. This may have been followed by an  
727 expansion of hypoxic waters, as recorded by simultaneous decreases of Mn and an increase of  
728 Fe/Mn and S together with the presence of *Arcella discooides*.

729

730 *5.4. Environmental and ecological conditions in Lake Apastepeque after the catastrophic 13<sup>th</sup>*  
731 *February 2001 earthquake (geological event I, 2–0 cm, beginning of the 21 century)*

732 Geological event I (GE I, Fig. 2), is characterized by the most significant shift within  
733 the biota records, indicating an abrupt alteration of the aquatic ecosystem. The most  
734 prominent change was observed in the cladoceran assemblage. Large bodied species  
735 characterize the system during GE I (after the earthquake) with Bosminidae species (size 0.2–  
736 1 mm) replaced by *Daphnia laevis* (size 1–2.5 mm). We also recorded the presence of *Moina*  
737 sp. ehippia which indicates high water turbidity and limited presence of fish as species of  
738 this genus are large and avoid fish presence. Furthermore, abundances of the diatom *A.*  
739 *granulata* suddenly increases. This species has often been associated with eutrophic, turbid,  
740 and turbulent water bodies as well as high physical alterations, for example as a consequence  
741 of erosion events (Kilham et al., 1986). Subsequently, highest sulphur concentrations and  
742 Fe/Mn values were noted indicating the depletion of oxygen (Boyle, 2001).

743 We suggest that these alterations were associated with a dramatic earthquake at the  
744 beginning of 2001 that was unprecedented in the study area over the investigation period. On  
745 13<sup>th</sup> January 2001 and 13<sup>th</sup> February 2001, two earthquakes of different origin with  
746 magnitudes of M<sub>w</sub>=7.7 and M<sub>w</sub>=6.6, respectively, occurred and caused severe damage to  
747 ecosystems and human settlements in El Salvador (Bommer et al., 2002). The most significant  
748 for Lake Apastepeque, however, was likely the second, slightly weaker earthquake (M<sub>w</sub>=6.6).  
749 The first one was caused by the subduction of the Cocos plate with its epicentre near to the  
750 continental shore, deep below the surface (ca. 60 km) and relatively distant to Lake  
751 Apastepeque (ca. 90 km). The second earthquake, on the other hand, was an upper-crust  
752 earthquake with a shallow epicentre (ca. 10 km), caused by rupture of a part of the fault-zone  
753 (Corti et al., 2005) which runs by the Apastepeque Volcanic Field. It was situated only about  
754 30 km away from the study site (Fig. 1).



755 Besides the widely reported loss of buildings and human population (ReliefWeb,  
756 2001), the earthquake on 13<sup>th</sup> February 2001 had a series of environmental consequences. The  
757 shaking caused localized, shallow landslides (Baum et al., 2001) with more than twenty-five  
758 landslides reported on the flanks of the San Vicente volcano alone (Global Volcanism  
759 Program, 2009). Furthermore, it generated liquefaction and, in turn, lateral displacement of  
760 the ground on lake shores, e.g., Lago de Ilopango (Baum et al., 2001). In Lake Apastepeque,  
761 mixing of the water column and likely liquefaction on the shores may have resulted in the  
762 release of toxic substances such as hydrogen sulfide, an alteration in water colour and  
763 transparency (from transparent to green, reduced light availability), increased extent of the  
764 anoxic zone, as well as a massive fish kill observed after earthquake on 13<sup>th</sup> February 2001  
765 (BLOG, 2021 – access no longer available; GoogleSite, 2015 – data provided by Turicentro  
766 Laguna de Apastepeque). These local reports along with our results allow us to deduce that  
767 GE I likely coincided with the environmental transformation caused by the earthquake of 13<sup>th</sup>  
768 February 2001. Importantly, the earthquake-induced water mixing could have been intensified  
769 by strong winds during the dry season that sometimes leads to complete turnover even of  
770 deep, crater lakes, e.g. Lake Rio Cuarto (Umaña et al., 1999).

771 The region of Lake Apastepeque is a highly seismic zone, and 68 upper-crust  
772 earthquakes with magnitudes between M 5.7–6.93 have taken place since AD 1528 in El  
773 Salvador and neighbouring countries (Salazar, 2021). However, only the second earthquake  
774 seems to have affected Lake Apastepeque. This assumption is supported by the noted fish kill  
775 event after the earthquake on 13<sup>th</sup> February 2001. We hypothesize that the strong impact of  
776 this event on Lake Apastepeque is a result of three combined factors: the upper-crust origin,  
777 the high magnitude and its close proximity to the lake. This hypothesis is supported by the  
778 fact that shallow crustal earthquakes cause more damage than deep, subduction earthquakes  
779 (Bent and Evans, 2004).

780 *5.5. Lake recovery after earthquake disturbance (zone III, surface sediments collected using*  
781 *Ekman grab, ca. AD 2013)*

782 Within the cladoceran assemblage, *Liederobosmina* sp. and *Bosmina* sp. have reappeared  
783 along with some new taxa such as *Chydorus* cf. *sphaericus*, *Graptoleberis testudinaria* and  
784 *Leydigia louisiana louisiana*. At the same time, *Daphnia laevis* and *Moina* sp. almost disappeared,  
785 probably because of fish reintroduction and predation (Fig. 2). The diatom assemblage

786 indicates a shift towards reduced turbulence and increased light availability by the almost total  
787 disappearance of *Aulacoseira granulata* var. *granulata*. Simultaneously, the benthic  
788 *Achnantheidium minutissimum*, which is often reported as a pioneer diatom taxon in disturbed  
789 environments (Peterson and Stevenson, 1992), occurred more abundantly together with  
790 several new taxa (e.g. *Achnantheidium* cf. *saprophilum*, *Achnantheidium straubianum*) (Fig.  
791 S8). Cladoceran and diatom analyses from surface sediments, accumulated since 2013,  
792 therefore suggest a partial recovery of the lake ecosystem after the earthquake. Nonetheless,  
793 the newly introduced taxa document a persistent effect of this catastrophic event on the  
794 aquatic ecosystem, even after several years.

## 795 **6. Conclusions**

796 Climatic variations over the last 500 years were manifested in Lake Apastepeque by  
797 fluctuating lake levels with a tendency towards high water level during the Little Ice Age,  
798 while multiproxy data document a short interval of drier climate in the older part of the LIA.  
799 These data support drier conditions during the Spörer minimum comparable to studies from  
800 Mexico and Belize. Subsequently, the climate that persisted throughout most of the LIA  
801 seems to have been relatively humid in the mid-elevations of El Salvador. The data from Lake  
802 Apastepeque, along with other palaeorecords covering the LIA from Central America and the  
803 circum-Caribbean region, displays a large diversity, and there remains no consensus  
804 regarding the regional pattern of climate changes. Climatic expression in this region seems to  
805 be significantly modified by local variables such as topography and altitude.

806 In spite of the significant role of the LIA in shaping environmental conditions and  
807 aquatic ecosystems, the most dramatic and abrupt changes in Lake Apastepeque, over the last  
808 530 years, were caused by a nearby earthquake on the 13<sup>th</sup> February 2001. This catastrophic  
809 event temporarily led to the total reorganization of lake biota, although some recovery is  
810 observable in more recent sediments.

811

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828

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## 1159 **Figure captions**

1160 **Figure 1.** Location map of Lake Apastepeque in El Salvador: a) position of the study area in  
1161 Central America.

1162 **Figure 2.** Summary diagram of aquatic proxies and main zones and event of lake evolution  
1163 during the last ca. 530 yr. Selected biotic and geochemical features of the record were  
1164 grouped by environmental, explanatory factors, where “+” means more positive relationship  
1165 of a given palaeoindicator with environmental factor, and “-” means more negative  
1166 relationship. The uppermost layer of Zone III encompasses surface sediments collected by  
1167 Ekman grab. Fe, Mn, Mg, Ca, S and PO<sub>4</sub> were determined by ICP-OES spectrometer. TOC  
1168 was determined by an elementary analyzer.

1169 **Figure 3.** Possible scenario of water level fluctuation in Lake Apastepeque during the Little  
1170 Ice Age: Scenario 1 - lake level drop, Scenario 2 - lake level rise.

1171 **Figure 4.** Map showing paleorecords including information about climatic conditions during  
1172 the Little Ice Age (LIA). Different color of dots indicates reconstructed climate conditions.  
1173 Red: drier conditions, blue: wetter/higher moisture availability and/or lower  
1174 evapotranspiration, yellow: wetter/higher moisture availability and/or lower  
1175 evapotranspiration with marked drier beginning of the LIA, red-blue: not clear signal. Black  
1176 dots: mainly temperature reconstructions. Gray arrows: direction of wind adapted from  
1177 Kilbourne et al. (2008). Numbers corresponding to discussed records: 1. Lake Santa María del  
1178 Oro (Rodríguez-Ramírez et al., 2015); 2. Lakes La Luna and El Sol (Cuna et al., 2014); 3.  
1179 Lake Metztitlán (Olivares-Casillas et al., 2021); 4. Lago Verde (Lozano-García et al., 2007);  
1180 5. Lago Aljojuca (Bhattacharya and Byrne, 2016); 6. Laguna San Lorenzo (Franco-Gaviria et  
1181 al., 2018b); 7. Laguna Esmeralda (Franco-Gaviria et al., 2018b); 8. Lake Lacandón (Vázquez-  
1182 Molina et al., 2016); 9. Aguada X’caamal (Hodell et al., 2005); 10. Tecoh cave-stalagmite  
1183 (Medina-Elizalde et al., 2010); 11. Mangrove sediments record (Aragón-Moreno et al., 2012);

1184 12. Lake Punta Laguna (Curtis et al., 1996); 13. Lake Salpetén (Rosenmeier et al., 2002); 14.  
1185 Lake Petén Itzá (Pérez et al., 2010); 15. Cave Macal Chasm (Webster et al., 2007); 16. Blue  
1186 Hole (Gischler et al., 2008); 17. Lake Izabal (Obrist-Farner et al., 2022); 18. Lake Amatitlán  
1187 (Vélez et al., 2011); 19. Laguna Llano del Espino (Dull, 2004a); 20. Lake Apastepeque (this  
1188 study); 21. Lake El Gancho (Stansell et al., 2013, Harvey et al. 2019); 22. Lake Nicaragua  
1189 (Slate et al., 2013); 23. Laguna Zoncho (Clement and Horn 2001; Lane et al. 2004; Haberyan  
1190 and Horn, 2005; Wu et al., 2016); 24. Lake San Carlos (Correa-Metrio et al., 2016); 25. Lake  
1191 Valencia (Curtis et al., 1999); 26. marine sediment cores, Cariaco Basin (Haug et al., 2001;  
1192 Black et al., 2007); 27. marine sediment core/corals reef (Winter et al., 2000; Nyberg et al.,  
1193 2002); 28. Lake Miragoane (Hodell et al., 1991); 29. unnamed lagoon (Peros et al., 2015); 30.  
1194 marine sediment core (Lund and Curry, 2006); 31. marine sediment core, Fisk Basin (Richey  
1195 et al., 2009); 32. marine sediment core, Garrison Basin (Richey et al., 2009). Detailed  
1196 information about the gathered records may be find in the Table S4 (supplementary material).