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1 Increased rainfall in southern Central 2 America under glacial climate 3 conditions

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10

11 **Abstract**

12 Late Pleistocene hydroclimate variability in Central America and its associated climate
13 forcings are poorly constrained. The region is influenced by complex
14 ocean-atmosphere-continent interactions, and documented palaeohydrological responses,
15 which vary by site and/or proxy specificity, are far from conclusive. We used δD of n-alkanes
16 from a marine sediment core in the Panama Basin to infer past changes in precipitation over
17 the last 56 kyr. Our results indicate a progressive intensification of precipitation during the last
18 glacial period, culminating in a precipitation maximum during the Last Glacial Maximum
19 (LGM, 23-19 kyr BP), followed by a rapid decline during the Heinrich Event 1 (H1, 18-15 kyr
20 BP) time interval. While the regional pattern of the precipitation anomaly during the LGM is
21 proxy and site dependent, the regional drying during H1 shows a clear north-south signature
22 associated with the southward meridional migration of the Intertropical Convergence Zone

23 (ITCZ). Using iTrace and PMIP4 model simulations, we show that the precipitation changes
24 associated with the ITCZ shift are closely linked to the equatorial SST front induced by
25 changes in the oceanic circulation. We propose that an increase in this latitudinal SST
26 gradient could have locally pushed the ITCZ further north, bringing rainfall to southern
27 Central America during the LGM.

28 **Keywords:**

29 plant waxes isotopic composition, hydroclimate, Last Glacial Maximum, Central America,
30 Intertropical Convergence Zone, ocean-atmosphere interactions

31

32 **1 Introduction**

33 Tropical regions, where the highest total rainfall occurs, host more than half of the world's
34 population. However, tropical rainfall is one of the most difficult parameters to simulate with
35 climate models (Douville et al., 2021). Atmospheric convection and its associated rainfall
36 occur above the warmest regions in the tropical ocean realm, so that any change in the
37 regional pattern of the tropical warm pools could have a profound impact on regional rainfall
38 (Tierney et al., 2013).

39 Warm pools are specific areas in the global ocean where the sea surface temperature (SST)
40 remains above 28.5°C throughout the year. Around the equator, three high precipitation
41 hotspots develop above the warm pools, located over Central America, the Indonesian region
42 and equatorial Africa (Trenberth and Shea, 2005). These precipitation maxima are associated
43 with large-scale meridional and zonal atmospheric structures that vary on seasonal and
44 interannual scales (Schneider et al., 2014). Central America lies at the core of the Western
45 Hemisphere Warm Pool (WHWP), which is divided into two oceanic regions: the Eastern
46 Pacific Warm Pool (EPWP) and the Atlantic Warm Pool. Central America makes the WHWP

47 span two oceans and sets up complex regional interactions between land, atmosphere and
48 ocean processes.

49 These characteristics make it difficult to assess the regional response of precipitation to
50 global climate change in the WHWP. For example, palaeoclimatic simulations of the Last
51 Glacial Maximum (LGM) provide contrasting hydroclimatic conditions in the WHWP region,
52 as the sign of LGM precipitation changes are model-dependent (Kageyama et al., 2021).
53 Globally, the ITCZ is thought to have migrated towards the warmest hemisphere above
54 oceans, with latitudinal shifts of about 1° during the LGM and with a notable additional
55 southward shift during Heinrich Event 1 (H1, McGee et al., 2014), while terrestrial
56 precipitation responds thermodynamically to monsoon systems occurring over continental
57 landmasses (Singarayer et al., 2017).

58 Reconstructions of tropical rainfall dynamics and the associated meridional position and/or
59 expansion of the ITCZ have led to alternating interpretations, leading to an unclear picture of
60 palaeoprecipitation evolution in the tropical American region. Regionally, Rincón-Martínez et
61 al. (2010) reported a northward shift of the ITCZ in the eastern equatorial Pacific (EEP) for
62 the LGM relative to today, while Arbuszewski et al. (2013) reported a southward shift of the
63 ITCZ in the equatorial Atlantic. However, these records are located far from the WHWP, and
64 other records from the area are either salinity based and provide contrasting results (**Figure**
65 **S1**), or do not cover the entire last glacial termination (Lachniet et al., 2009).

66 The aim of this study is to assess the spatial patterns of precipitation variability in Central
67 America during the LGM and to identify the climatic drivers of these precipitation patterns. We
68 present a precipitation reconstruction of Central America by analysing plant wax from a
69 marine sediment core collected in the Panama Basin, which traces changes in precipitation
70 over the adjacent continent over the last 56 kyrs. The MD02-2529 core is ideally located in
71 the WHWP, an area where records of LGM and deglacial atmospheric hydroclimate are

72 lacking. Our results provide insights into the past hydroclimatic cycle of Central America,
73 which we explain by analysing PMIP4 model simulations of the LGM (Kageyama et al.,
74 2021). We identify an ocean-atmosphere interaction in the EEP, where the latitudinal SST
75 gradient drives rainfall changes in the warm pool region.

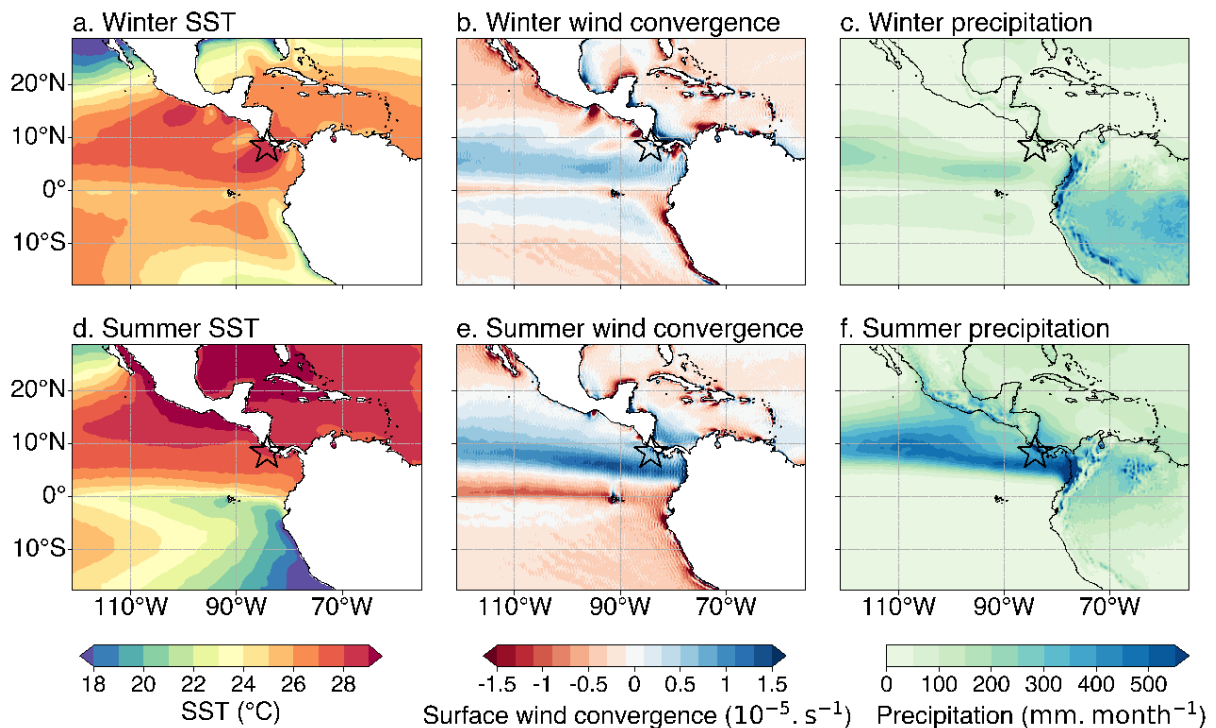
76 **2 Regional climatology**

77 MD02-2529 was collected in the EEP 08°12.33' N, 84°07.32' W, 1619 m water depth
78 (Beaufort et al., 2002). The surface waters of the EEP are characterised by two strong
79 gradients in sea surface temperature (SST). The northern EEP is characterised by warm and
80 stratified surface waters as part of the Eastern Pacific Warm Pool (EPWP), which extends
81 along the coast of central Mexico to Nicaragua with SST warmer than 28.5°C (**Figure 1**). This
82 EPWP is the Pacific part of the larger WHWP, which includes the EPWP, the Caribbean Sea
83 and part of the Gulf of Mexico (Wang & Enfield, 2001). Further south, a strong front separates
84 the EPWP from the colder waters of the equatorial cold tongue (**Figure 1d**). The equatorial
85 front is one of the steepest SST gradients in the world. The spatial and temporal variations in
86 precipitation are mainly driven by changes in the SST patterns in the EEP, which influence
87 the regional wind stress convergence (Chelton, 2001) and the resulting ITCZ.

88 At the seasonal scale, precipitation patterns in southern Central America are characterised
89 by a dry season during the boreal winter and a wet season during the boreal summer (**Figure**
90 **1**), resulting from the latitudinal shift of the ITCZ (**Figure 1c, f**). The wet season is interrupted
91 in July during the midsummer drought, resulting in a bimodal wet season with two
92 precipitation maxima in May-June and September-October (**Figure 2a**).

93 Interbasin changes in the SST pattern also influence moisture transport across the isthmus
94 from the Atlantic to the Pacific (Leduc et al., 2007). The Caribbean low-level jet (**Figure S2a**),
95 a trade wind that originates in the Atlantic and is mainly active from June to August (Amador
96 et al., 2006), is the main moisture conveyor across the isthmus (Durán-Quesada et al., 2010).

97 The low-level circulation also consists of the Choco low-level jet, a westerly wind that blows
 98 along the Peruvian coast and changes direction as it crosses the equator, bringing moisture
 99 to the isthmus from September to November (Poveda and Mesa, 2000, **Figure S2b**). On an
 100 interannual timescale, the El Niño Southern Oscillation (ENSO) is the main mode of SST
 101 variability in the EEP and drastically affects the cold tongue region (Rasmusson and
 102 Carpenter, 1982). El Niño warm events manifest as a precipitation deficit in the Pacific region
 103 and as a precipitation intensification in the Caribbean region (Sánchez-Murillo et al., 2017).
 104 However, along the Costa Rican margin, El Niño years only slightly alter the annual cycle of
 105 rainfall rates and their isotopic composition (Linsley et al., 1994).



106

107 **Figure 1.** Modern climatology of Central America and adjacent Eastern Equatorial Pacific
 108 ocean. **a, d:** SST ($^{\circ}\text{C}$); **b, e:** Surface wind convergence ($10^{-5} \cdot \text{s}^{-1}$); **c, f:** Precipitation rates
 109 ($\text{mm} \cdot \text{month}^{-1}$) for boreal winter (January, February, March, upper panels) and summer (July,
 110 August, September, lower panels). The star indicates the position of core MD02-2529. Data
 111 from ERA5 (Hersbach et al., 2023).

112 **3 Material and Methods**

113 **3.1 Chronology**

114 The chronology for core MD02-2529 has been modified from Leduc et al. (2007), in particular
115 with the addition of three radiocarbon dates for the Holocene time window indicating a
116 mislabelled section on board during the MONA cruise (see Supplementary Text 1 and **Figure**
117 **S3**).

118 We now have fourteen radiocarbon dates for the planktonic foraminiferal species
119 *Neogloboquadrina dutertrei*. Of these fourteen radiocarbon dates, two were separated by
120 only 1 cm in the sedimentary sequence and gave virtually the same age (Leduc et al., 2007);
121 we therefore merged these two radiocarbon dates for the final age model, which contains
122 thirteen radiocarbon-based age control points (**Table S1**). We used the Bacon package on R
123 software (Blaauw and Christen, 2011, **Figure S4**) to calibrate radiocarbon ages against the
124 Marine20 radiocarbon calibration curve (Heaton et al., 2020), taking into account the local
125 reservoir age ΔR of -72 ± 94 yr for the surface water mass at the core site
126 (<http://calib.org/marine/>). To obtain additional age control points beyond the radiocarbon age
127 limit, we used isotope stratigraphy as described in Leduc et al. (2007), but with the updated
128 Greenland and Antarctic ice core timescales GICC05 published in Svensson et al. (2020).

129 **3.2 *n*-alkanes extraction and quantification**

130 Total lipids were extracted from 5 to 10 g of freeze-dried sediment using an Accelerated
131 Solvent Extractor (ASE 350, Thermo Scientific), with a dichloromethane/methanol mixture of
132 9:1. Known amounts of squalane and C₃₆ *n*-alkane were added prior to extraction as internal
133 standards. Total lipid extracts (TLE) were eluted with hexane on silica gel column
134 chromatography yielding the apolar (F1) fraction including *n*-alkanes. F1 was then purified on
135 an Ag-Si column with hexane. *n*-alkanes were quantified by comparing the integrated peak
136 areas with those of the C₃₆ *n*-alkane internal standard using a Thermo Scientific Trace GC

137 gas chromatograph (GC) equipped with a DB-5-MS (J&W) column (60 m x 0.25 mm x 0.1
138 μm) fitted with a 2.5 m x 0.53 μm deactivated retention gap, using hydrogen as a carrier gas
139 and a flame ionization detector (FID).

140 3.3 Compound-specific carbon and hydrogen stable isotope 141 analysis

142 Compound-specific stable hydrogen (δD) and carbon isotope ($\delta^{13}\text{C}$) analysis of long chain
143 *n*-alkanes was performed at CEREGE on a Thermo Scientific Trace GC coupled via a GC
144 Isolink II conversion unit to a Thermo Fisher Scientific Delta V⁺ mass spectrometer. The GC
145 was equipped with a TG5ms (30 m x 0.25 mm x 0.25 μm column) and Helium was used as
146 the carrier gas. The GC temperature was programmed to increase from 80°C to 180°C at
147 10°C/min and then at 5°C/min to 315°C (held 16 min). The HTC pyrolysis reactor was held at
148 1420°C for hydrogen analysis and the combustion reaction was held at 1000°C for carbon
149 analysis.

150 The samples were injected in random stratigraphic order in duplicate. Due to low
151 concentrations of sedimentary *n*-alkanes, around 30% of the data produced mass
152 spectrometer signals below 2 V and were excluded. Nonetheless, the C₂₉ and C₃₁ *n*-alkane
153 homologues exhibit almost identical δD variations, despite having different abundances,
154 suggesting that the isotopic signal as a whole is not impacted by small amounts of *n*-alkanes.

155 Instrument performance and the H₃⁺ factor were monitored on a daily basis using a reference
156 H₂ gas and a mixture of *n*-alkanes of known isotopic composition. The H₃⁺ factor (Sessions et
157 al., 2001) was 5.5 ± 0.09 during the analysis period. The *n*-alkane mixture A7 (provided by
158 Arndt Schimmelmann; Indiana University) was used as an external standard mixture. It was
159 analysed in duplicate repeatedly every six injections to monitor potential deviation throughout
160 a sequence of analysis and the entire period of analysis. Additional injections of an internal
161 sedimentary standard (from Lake Chad) were also monitored for each sequence of analysis.

162 All the A7 mix, Lake Chad and the squalane recovery standard indicate a standard deviation
163 of δD and $\delta^{13}C$ better than 2 ‰ and 0.4 ‰, respectively. δD and $\delta^{13}C$ are given in ‰ relative
164 to Vienna Standard Mean Ocean Water (V-SMOW) and Vienna Pee Dee Belemnite (V-PDB),
165 respectively.

166 3.4 PMIP4 models

167 We have used the available model results from the latest generation of PMIP experiments
168 (PMIP4; Kageyama et al., 2021), most of which are part of the Coupled Model
169 Intercomparison Project phase 6 (CMIP6). The database now also includes CESM2.1 (Zhu et
170 al., 2021a), which has been processed like all other models published in Kageyama et al.
171 (2021). The LGM model outputs analysed here are from the PMIP4-CMIP6 LGM experiments
172 (Kageyama et al., 2017). We use the corresponding pre-industrial (PI) control experiments as
173 a reference. The LGM boundary conditions differ from those of the PI period mainly due to
174 reduced atmospheric concentrations of greenhouse gases, lower sea level, the presence of
175 large continental ice sheets and an orbital configuration set at 21 kyr BP (Kageyama et al.,
176 2017).

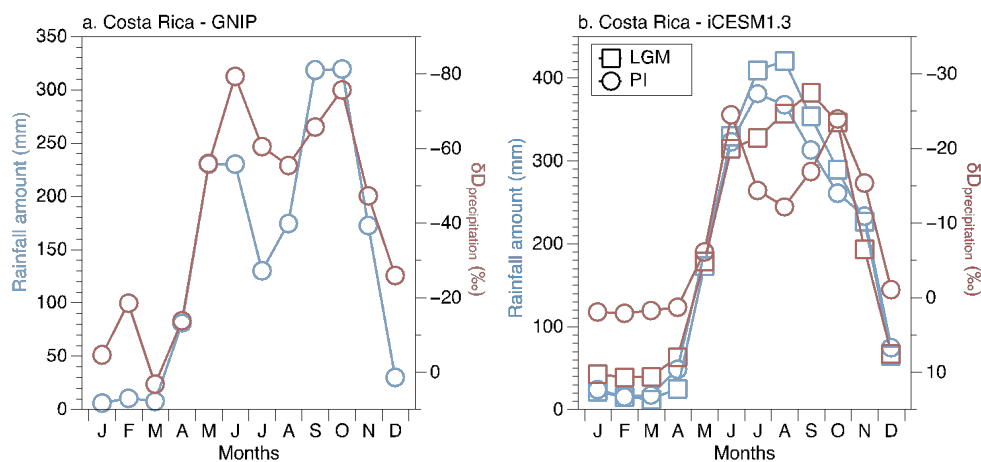
177 SST and total precipitation data from 13 different models were obtained from the CMIP6
178 ESGF database and the PMIP4 database (<http://dods.lsce.ipsl.fr/pmip4/db/>). The 13 models
179 using the PMIP4 protocol are the 12 models UoF-CCSM4, MIROC-ES2L, HadCM3 ICE-6G,
180 HadCM3 GLAC-1D, CESM1.2, AWIESM1, AWIESM2, INM-CM4-8, iLOVECLIM GLAC-1D,
181 iLOVECLIM ICE-6G, MPI-ESM1.2 and IPSL-CM5A2 presented in Kageyama et al. (2021)
182 and the CESM2.1 simulation from Zhu et al. (2021a). We defined large enough geographical
183 areas to compute regional averages that are representative of the regions of interest. We
184 delimited two SST regions for the calculation of latitudinal SST gradients in the EEP, i.e. the
185 cold tongue (5°S-0°, 93°W-83°W) and the EPWP (7°N-12°N, 97°W-87°W), and two
186 precipitation regions for the detection of latitudinal shifts in the ITCZ (0°N-5°N, 95°W-85°W
187 and 8°N-13°N, 95°W-85°W, see red and black rectangles in **Figure 6**). The southern ITCZ

188 position corresponds to the southernmost position of the modern ITCZ (**Figure 1c**) and the
 189 northern ITCZ position corresponds to the northernmost position of the modern ITCZ (**Figure**
 190 **1f**). To keep the calculations consistent, we have chosen a fixed location of these
 191 geographical areas to calculate the gradients of SST and precipitation for all models, even
 192 though the reproduction of these zonal patterns can vary between models by a few degrees
 193 of latitude. In addition to oceanic and climatic variability, averaging the boxes used to
 194 calculate the model-derived sea surface temperature (SST) and precipitation gradients
 195 mitigates disparities in the spatial resolution of the different models.

196 3.5 iTrace simulation

197 The iTrace simulation is a transient simulation covering the period from 20 to 11 kyr BP (He
 198 et al., 2021, data available at <https://doi.org/10.26024/b290-an76>). It uses iCESM1.2, an
 199 isotope-enabled coupled GCM (Brady et al., 2019) with the control experiments iCESM1.3
 200 LGM and PI from Zhu et al. (2017). We use the iTrace core experiment version, which
 201 includes the evolving orbital conditions, ice sheets, greenhouse gases and meltwater of the
 202 run (He et al., 2021).

203 The iCESM1.3 PI control and LGM experiments reproduce the seasonal cycle of precipitation
 204 rates and the amount effect on precipitation δD , albeit without the mid-summer dry season
 205 and with an anomalously low magnitude of seasonal δD changes (**Figure 2**).



206

207 **Figure 2.** Modern climatology over Costa Rica in GNIP data and comparison with iCESM1.3
208 (ITRACE control experiment). (a) Monthly precipitation amount ($\text{mm}\cdot\text{month}^{-1}$) and associated
209 δD of precipitation (‰) in Costa Rica. Monthly GNIP data from Heredia station in Costa Rica
210 averaged during the 2013-2020 period (IAEA/WMO, 2024). (b) iCESM1.3 (Zhu et al., 2017)
211 precipitation amount ($\text{mm}\cdot\text{month}^{-1}$) and δD of precipitation (‰) in Costa Rica (at 8.5°N ,
212 82.5°W) for the PI control simulation (circles) and the LGM simulation (squares). Note the
213 difference in y scaling in a and b because the magnitude of the δD precipitation seasonality in
214 the iCESM1.3 model is damped compared to the GNIP isotopic data.

215 **4 Results**

216 **4.1 *n*-alkane concentrations**

217 Plant wax long chain *n*-alkanes are derived from the epicuticular waxes of terrestrial higher
218 plants (see e.g. Sachse et al., 2012). The average sedimentary concentrations of the four
219 dominant long-chain odd-numbered *n*-alkanes of core MD02-2529 are approximately 80,
220 300, 320 and 170 $\text{ng}\cdot\text{g}^{-1}$ for *n*- C_{27} , *n*- C_{29} , *n*- C_{31} and *n*- C_{33} , respectively (**Figure 3a**). The two
221 most abundant are *n*- C_{29} and *n*- C_{31} , which vary from a minimum of 25 $\text{ng}\cdot\text{g}^{-1}$ to a maximum of
222 830 $\text{ng}\cdot\text{g}^{-1}$ for *n*- C_{29} and from 27 $\text{ng}\cdot\text{g}^{-1}$ to 920 $\text{ng}\cdot\text{g}^{-1}$ for *n*- C_{31} (**Figure 3a**).

223 All homologues share the same temporal trends, with maximum and minimum abundances
224 recorded during the LGM and the Holocene, respectively (**Figure 3a**). There is a marked
225 decrease in *n*- C_{29} and *n*- C_{31} concentrations between ~ 18 and 15 kyr BP, coeval with the
226 Heinrich event 1 chronozone. Conversely, the other Heinrich events that punctuated the MIS
227 3 period are not apparent in the *n*-alkane concentration changes.

228 **4.2 $\delta^{13}\text{C}$ of *n*-alkanes**

229 C_3 and C_4 physiological pathways lead to different $\delta^{13}\text{C}$ values of plant wax. A recent
230 literature review reports *n*-alkane $\delta^{13}\text{C}$ values for C_3 vegetation in tropical rainforest
231 environments of ~ -35 to -40 ‰ and values for C_4 grass of ~ -20 to -23 ‰ (Liu et al., 2022).

232 MD02-2529 *n*-C₂₉ and *n*-C₃₁ δ¹³C records vary from -35.0 ‰ to -31.7 ‰ (-33.8 ‰ on
233 average) and from -35.6 ‰ to -31.7 ‰ (-33.7 ‰ on average), respectively, without any
234 noticeable long-term trend (**Figure 3b**). These *n*-C₂₉ and *n*-C₃₁ values clearly indicate that
235 the vegetation type was predominantly a rainforest for the entire time interval studied (**Figure**
236 **3b**).

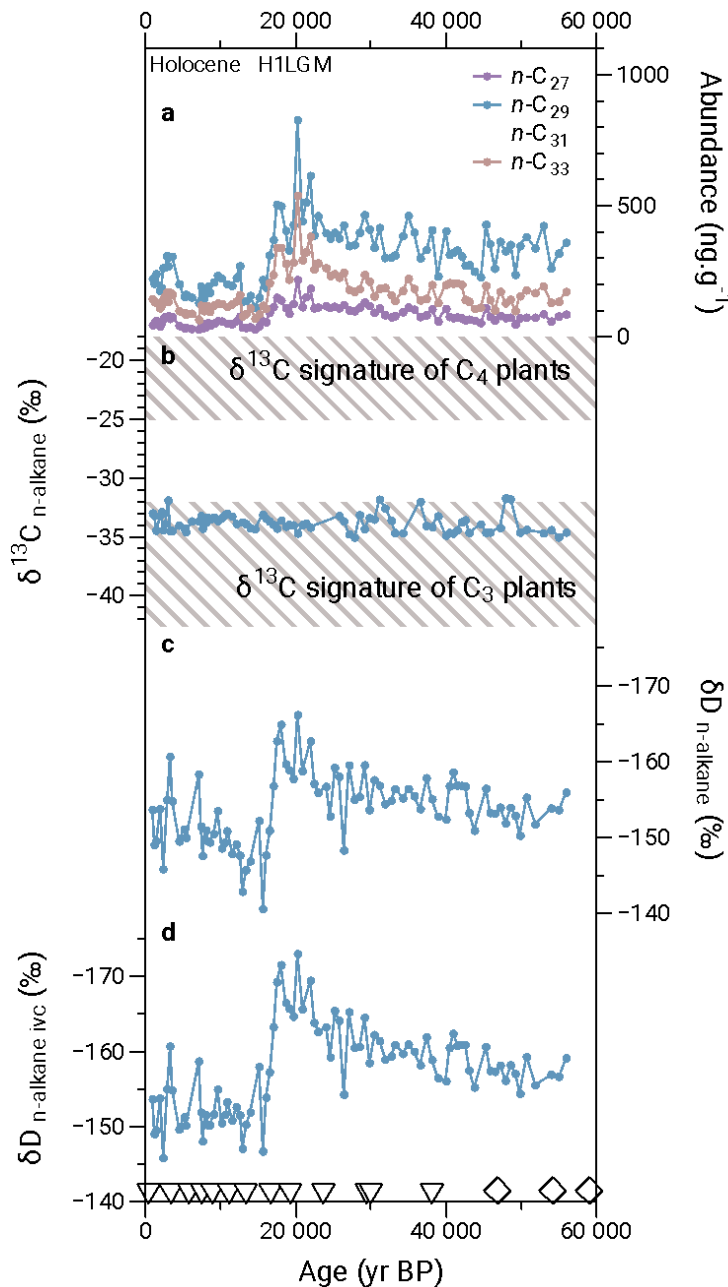
237 Changes in the relative proportion of the respective contributions of *n*-alkanes synthesised by
238 C₃ versus C₄ plants can also obscure the plant wax δD signal because both C₃ and C₄
239 physiological pathways do not have the same magnitude of apparent fractionation between
240 the isotopic signatures of water and plant wax (McInerney et al., 2011). The constant δ¹³C
241 values exclude the need to correct the δD values for changes in vegetation types that may
242 have altered the δD signal. We will assume that there is no variation in the C₃ and C₄
243 photosynthetic pathways of the plant types producing the analysed sedimentary plant waxes
244 and interpret the δD changes of the plant waxes as reflecting those associated with the δD of
245 environmental water.

246 4.3 δD of *n*-alkanes

247 *n*-C₂₉ and *n*-C₃₁ δD records vary from -166 to -141 ‰ (-154 ‰ on average) and from -166 to
248 -142 ‰ (-157 ‰ on average), respectively (**Figure 3c**). The isotopic δD compositions of the
249 two homologues exhibit the same temporal changes, with a long-term progressive isotopic
250 decrease for the 56-18 kyr BP time window, a subsequent sharp isotopic increase of about
251 20 ‰ co-occurring during the Heinrich event 1 chronozone, and a Holocene period marked
252 by the highest δD values during which we observe some multi-millennial δD fluctuations
253 (**Figure 3c**).

254 We corrected our δD *n*-alkane data from the global isotope changes in the water cycle on a
255 glacial-interglacial scale with the δ¹⁸O isotope values in Waelbroeck et al. (2002) with the
256 following conversion: $\delta D_{n\text{-alkane ivc}} = 8 \cdot \delta^{18}\text{O} \cdot (1 + \delta D_{n\text{-alk}} / 1000) / (1 + 8 \cdot \delta^{18}\text{O} / 1000)$ (**Figure 3d**). We

257 interpret the ice-volume corrected δD of n -alkanes ($\delta D_{n\text{-alkane ivc}}$) as a proxy for the δD of
 258 environmental water (Sachse et al., 2012). Once applied, the correction does not significantly
 259 reshape the changes observed in the raw $\delta D_{n\text{-alkane}}$, indicating that changes in ice volume
 260 have only a secondary effect on $\delta D_{n\text{-alkane}}$.



261

262 **Figure 3.** MD02-2529 n -alkanes analysis. (a) Abundance of the four dominant n -alkanes, (b)
 263 $\delta^{13}\text{C}$ $n\text{-C}_{29}$ and $n\text{-C}_{31}$, hatched areas represent the range of both C₃ and C₄ n -alkanes tropical

264 carbon isotopic signatures (Liu et al., 2022), (c) δD n -C₂₉ and n -C₃₁ values, and (d) δD n -C₂₉
265 and n -C₃₁ values corrected for ice volume changes. The age control points are displayed as
266 triangles (radiocarbon dating) and diamonds ($\delta^{18}O$ tie points).

267 **5 Discussion**

268 **5.1 Control on the plant wax sources**

269 Eolian, fluvial, and marine processes transport and deposit n -alkanes into the Panama Basin
270 sediments. Spatial distribution of multiple biomarkers of terrestrial origin in the Panama Basin
271 marine sediments indicate that river discharge is the main mode of transport of n -alkanes at
272 coring site (see Huguet et al., 2019 for discussion). We hypothesize that MD02-2529,
273 currently located 60 km away from the continent where tropical forests dominate continental
274 vegetation, are influenced by fluvial inputs of terrestrial organic matter. $\delta^{13}C$ values of
275 n -alkanes are in agreement with those from the tropical forest vegetation in Costa Rica
276 (Douglas et al., 2012). As there is no influence of lateral advection on *in-situ* oceanic
277 biomarkers (e.g. alkenones) in the Panama Basin (Kusch et al., 2010), we suppose negligible
278 lateral transport of previously deposited continental biomarkers that could overprint
279 syn-deposited n -alkanes.

280 Given that the measured wet bulk density is nearly constant downcore of MD02-2529
281 (Beaufort, 2002), that the carbonate, opal and organic carbon content is always below 15, 5
282 and 4% respectively (Leduc et al., 2010; Romero et al., 2011) and that sedimentation rate
283 changes smoothly from the mid-Holocene to the core bottom, we attribute the changes in
284 n -alkane concentration to changes in n -alkane fluxes mediated by wet transport from the
285 adjacent continent without significant changes in dilution by biogenic remains (**Figure S5**).
286 Even if MD02-2529 is only located 60 km away from the coast, the local continental margin is
287 so narrow that we could exclude significant changes in the distance of the marine core to the
288 coast during glacial periods to explain the increases in the n -alkane fluxes at coring site

289 (Harris et al., 2013). We thus directly interpret the *n*-alkane concentrations as reflecting the
290 intensity of *n*-alkanes delivery by regional riverine runoff.

291 5.2 Controls on the water isotopic signal recorded by terrestrial 292 plant *n*-alkanes

293 Leaf waxes ultimately record environmental water during biosynthesis before being fossilised
294 in sedimentary sequences, and δD in lipid biomarkers thus record the isotopic composition of
295 environmental water (Sauer et al., 2001), influenced by evaporation-precipitation processes
296 and specific biosynthetic fractionations during lipid biosynthesis (Sachse et al., 2012). On a
297 global scale, there is a direct relationship between the δD of *n*-alkanes and the δD of mean
298 annual precipitation (Sachse et al., 2012; Ladd et al., 2021).

299 In the tropics, the primary control on water isotopic composition of precipitation is the amount
300 effect (**Figure 2**), which corresponds to a negative relationship between precipitation amount
301 and the isotopic composition of precipitation (Dansgaard, 1964; Risi et al., 2008). However,
302 other processes such as cloud microphysics (Konecky et al., 2019), types of precipitation
303 (e.g. stratiform vs. convective, Aggarwal et al, 2016; Konecky et al., 2019), strength of deep
304 convection (Tharammal et al., 2017), origin and transport of moisture (Sánchez-Murillo et al.,
305 2016) can all affect the isotopic signal of precipitation. Regionally, monthly isotopic values of
306 precipitation in Belize, Guatemala (Lachniet and Patterson, 2009) and Costa Rica
307 (Sánchez-Murillo et al., 2013) indicate a primary influence of the amount effect, with a
308 secondary influence of the origin of moisture sources (Lachniet et al., 2007). El Niño warm
309 events do not exhibit any significant alteration in the monthly relationship between isotope
310 and precipitation amount (Sánchez-Murillo et al., 2017).

311 We hence interpret changes in $\delta D_{n\text{-alkane ivc}}$ in MD02-2529 as reflecting changes in precipitation
312 rate, with wetter (more negative δD) versus drier conditions (less negative δD) in southern
313 Central America.

314 5.3 Regional rainfall changes in Central America

315 Spatiotemporal changes in precipitation patterns are alternatively explained either by a
316 continental monsoon system associated with seasonal alternations of sea-land pressure
317 contrasts and their associated wind reversal, or by the seasonal latitudinal migration of the
318 ITCZ that mainly manifests above the warmest tropical ocean regions (Geen et al., 2020).
319 Global monsoon characterises tropical precipitation areas with strong seasonal contrasts and
320 a resulting wet season, whereas the ITCZ mainly tracks convective atmospheric variability
321 responsible for a narrow latitudinal band of particularly intense precipitation rates over
322 oceans (Geen et al., 2020).

323 In Central America, most of the climate forcings for the last glacial-interglacial transition have
324 already been used to explain past changes in precipitation, because the timing of
325 precipitation changes varied considerably in different subregions. In core MD02-2529, we
326 record a slight increase in precipitation in Costa Rica from 60 to 18 kyr BP, without much
327 variation during the glacial period, and with a dominant wet LGM. Precipitation decreases
328 during the H1 event and remains low during the Holocene compared to the LGM, with
329 additional multi-millennial variations. δD *n*-alkanes in the MD02-2529 core do not show a
330 strong response to local or high latitude insolation at the orbital scale. In the following
331 discussion, we focus on the major changes in the MD02-2529 record for the LGM and H1,
332 and compare them with regional palaeorecords of precipitation in a broader context (**Figure**
333 **4**, **Figure 5**, **Figure S6**). In particular, we focus on a region that extends beyond Central
334 America to include the Caribbean and northern South America.

335 5.3.1 LGM

336 Comparison of the LGM with the late Holocene isotopic record indicates a wetter LGM in
337 MD02-2529 (**Figure 4 e**) and Caracos cave in Colombia (Ramirez et al., 2023, **Figure 4 f**), a
338 slightly wetter than late Holocene LGM in SW Mexico (Lachniet et al., 2013, **Figure 4 c**), and
339 a drier than present-day LGM in NE Mexican, Cuban caves (Wright et al., 2023; Warken et

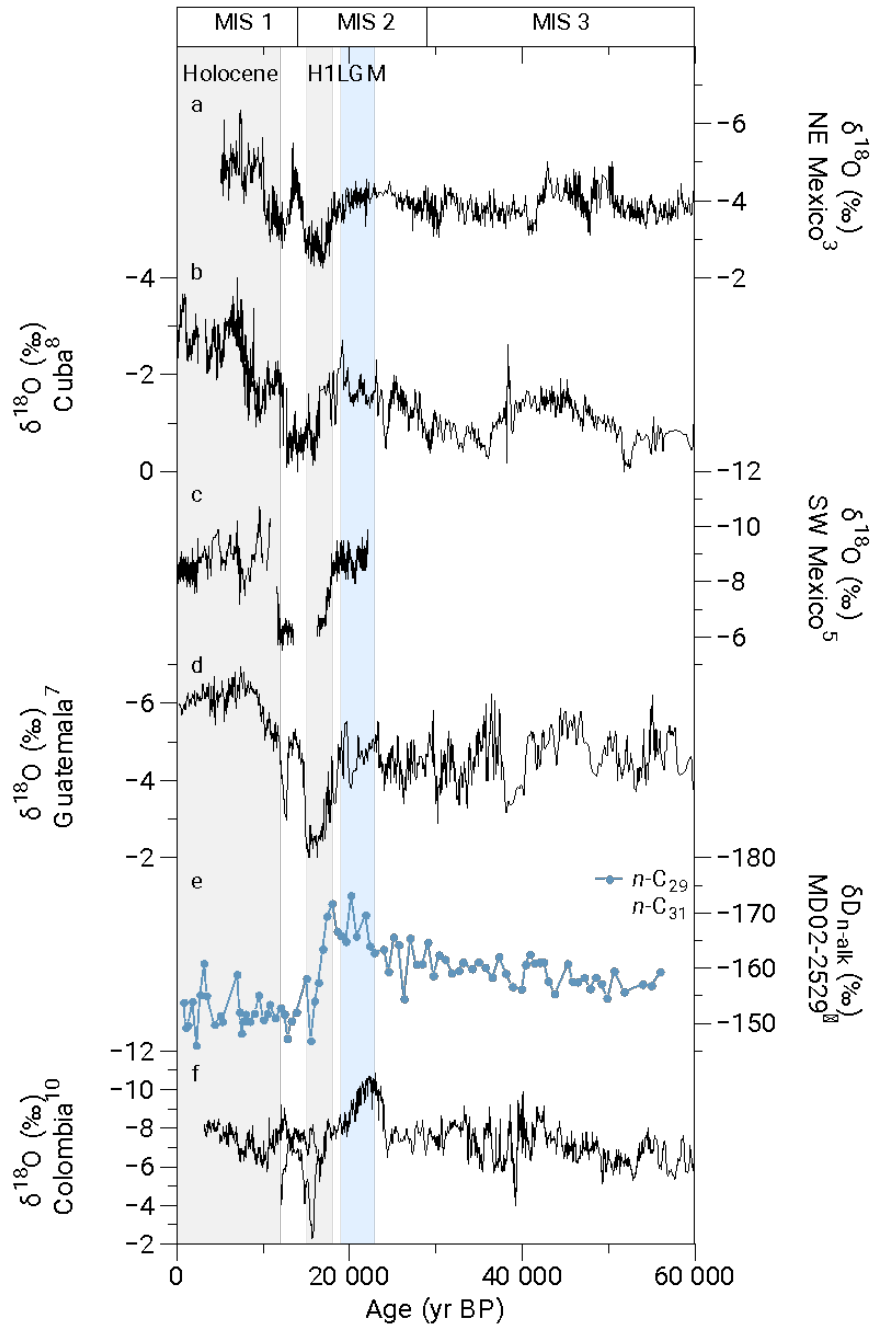
340 al., 2019, **Figure 4 a and b**) and Maya highlands caves (Lucia et al., 2024, **Figure 4 d**). It
341 highlights contrasting glacial-interglacial changes in precipitation intensity with respect to
342 latitude.

343 Interestingly, at Petén Itzá, Guatemala, the isotopic changes mimic those recorded in the
344 northern Mexican caves, but other proxies for rainfall all show different rainfall changes
345 (**Figure S6**). The first downcore record from Petén Itzá reported a wet LGM based on
346 downcore magnetic susceptibility and sediment density (Hodell et al., 2008). A wetter LGM is
347 further supported by isotopic and non-isotopic records, including pollen and diatom
348 assemblages (**Figure S6**). This suggests that the contrasting proxies analysed at Petén Itzá
349 have their own specificities and may preferentially record contrasting seasons, rainfall
350 regimes and/or other aspects of these sedimentary sequences.

351 5.3.2 H1 event

352 MD02-2529 δD *n*-alkanes is characterized by a wet-to-dry transition during the H1 event
353 (**Figure 3**). In all other isotopic records, the H1 event represents a dry climatic anomaly
354 (**Figure 4**). Other non-isotopic records suggest such a pattern, and the only record indicating
355 wetter conditions is located just south of the equator along the Pacific coast (Rincón-Martínez
356 et al., 2010, **Figure 5**).

357 In high-resolution records from the North Atlantic, the H1 event has two phases (Bard et al.,
358 2000). Some sites in tropical North America and the EEP also show multiple phases during
359 H1 (**Figure S7**). Some numerical studies investigating ocean-ice sheet interactions during
360 Heinrich events illustrate the complex processes likely to occur during Heinrich events
361 (Alvarez-Solas et al., 2010). However, the MD02-2529 *n*-alkane record does not allow us to
362 further investigate the complexity of the hydroclimate response of southern Central America
363 during the H1 event due to the resolution and additional uncertainties associated with the
364 changing reservoir age over time in the EEP (see, e.g., Zhao & Keigwin, 2018).



365

366 **Figure 4.** Comparison of (e) MD02-2529 δD n -alkanes ice volume corrected over the last 60
 367 kyr with hydroclimate records in tropical America based on isotopic records. Speleothem $\delta^{18}O$
 368 values in (a) Cueva Bonita, Mexico (Wright et al., 2023), (b) Santo Tomas cave and Dos Anas
 369 cave (Warken et al., 2019 and reference therein), Cuba ; (c) Juxtlahuaca cave and Cueva del
 370 Diablo (Lachniet et al., 2013 and reference therein), Mexico; (d) Maya highlands caves

371 (Grutas del Rey Marcos, Bombil Pek, and Jul Iq), Guatemala (Lucia et al., 2024 and
372 reference therein); (f) Caracos cave, El Peñon, Colombia (Ramirez et al., 2023). All isotopic
373 records are corrected for ice volume changes. Numbers associated with site labels are
374 reported on the map in **Figure 5**.

375 5.3.3 Model-data comparison using the iTrace modeling simulation

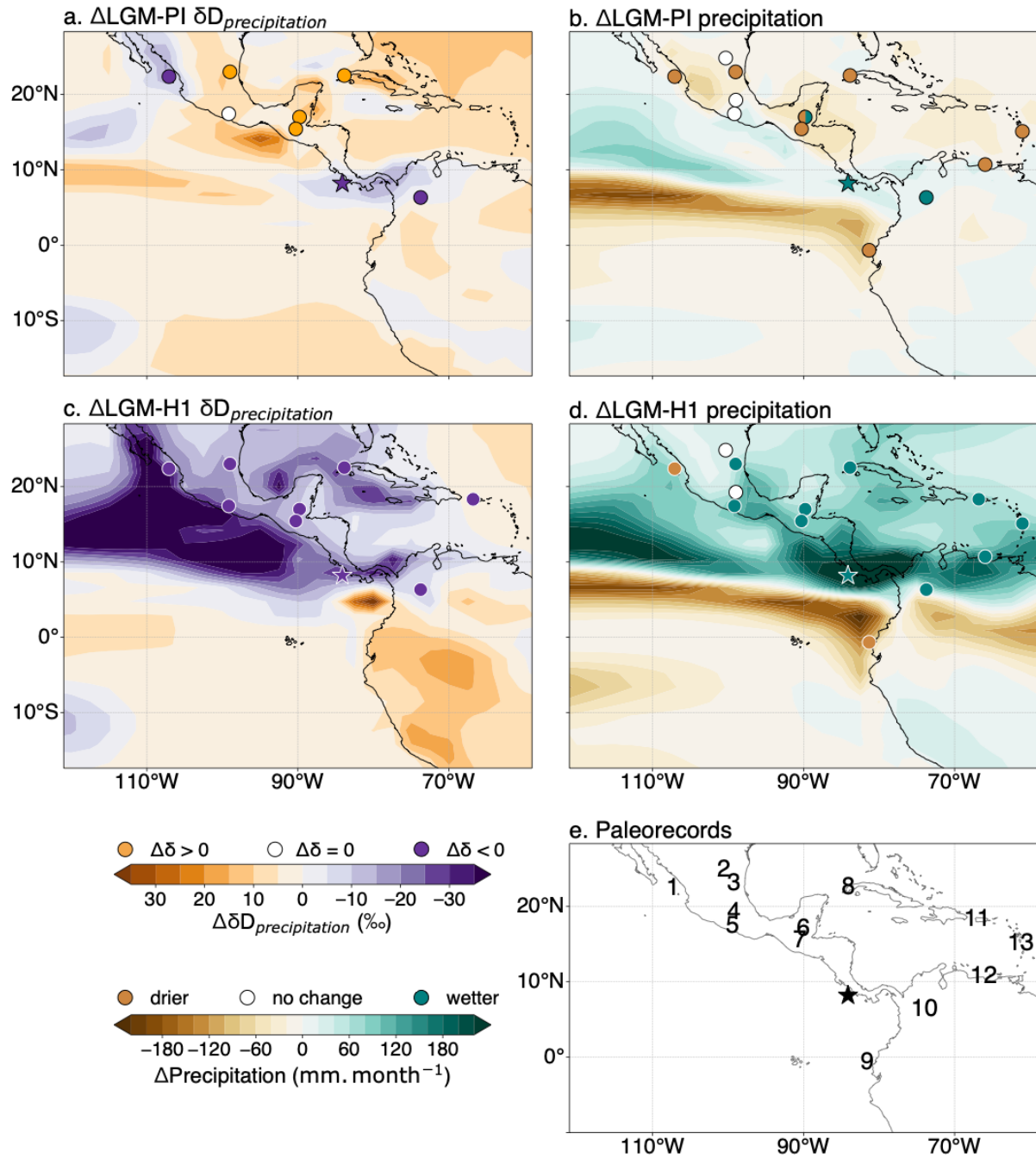
376 The full iTrace simulation (He et al., 2021) allows us to consider the LGM-PI and LGM-H1
377 anomalies to investigate the spatial diversity of precipitation patterns and associated water
378 isotope values. iTrace reproduces the LGM-PI anomaly over the continent near the coring
379 site both in δD of precipitation (more negative δD *n*-alkanes in the record during the LGM and
380 more negative δD precipitation in iCESM, **Figure 5a**) and in precipitation (**Figure 5b**). The
381 iTrace simulation also reproduces the LGM-H1 anomaly of the MD02-2529 δD *n*-alkanes
382 over the continent in both δD of precipitation (**Figure 5c**) and precipitation (**Figure 5d**).
383 These results are consistent with the tropical response to Heinrich events (Bradley and Diaz,
384 2021) and the southward shift of the ITCZ due to North Atlantic cooling.

385 Spatial comparisons between δD precipitation and precipitation rate agree in the sign of the
386 LGM-H1 anomaly (**Figures 5a and 5b**) over continental Central America, with more negative
387 δD where LGM precipitation is higher than H1 precipitation. The LGM-PI anomaly (**Figure 5a**
388 **and 5b**) is less pronounced than the LGM-H1 anomaly (**Figure 5c and 5d**), but the δD
389 precipitation is still consistent with the sign of the changes, although not in magnitude when
390 comparing the iCESM model and our data. Both isotopic anomalies (**Figures 5a and 5c**) and
391 hydroclimate interpretations (**Figures 5b and 5d**) agree with the sign of change between
392 LGM and PI (**Figure 5a and 5b**) and LGM and H1 (**Figure 5b and 5d**) iTrace model
393 simulation.

394 5.4 A mechanism for a wet LGM in southern Central America

395 5.4.1 Ocean-atmosphere mechanism

396 Oceanic features influence atmospheric circulation above the EEP and the adjoining
397 continent. Increasing atmospheric temperatures make their water-holding capacity increase.
398 At the coring site, summer winds crossing the equator blow over the cold tongue SST
399 gradient before converging above the Panama Basin where both SST and the air reaches
400 temperatures much higher than those found in the cold tongue and further South (**Figure 1**).
401 Eventually, wind convergence occurs at around 5°N downwind of the SST front, and
402 convergence maxima co-occur with that of precipitation (**Figure 1**).



403

404 **Figure 5.** Synthetic map representing the extracted precipitation (b and d) and its associated
 405 δD of precipitation (a and c) as simulated by iCESM (Zhu et al., 2017) for the boreal summer
 406 (July, August and September) in the full iTrace simulation (He et al., 2021). Maps were
 407 computed for the LGM-PI (a and b) and LGM-H1 (c and d) anomalies. iTrace time intervals
 408 are defined as follows: LGM and PI control experiments from Zhu et al. (2017), H1 from 16 to
 409 15 kyr BP iTrace (He et al., 2021). Dot colours indicate the sign of hydroclimatic changes as

410 reported in each original publication listed in the Supplementary Data. (e) Archives - star:
411 MD02-2529 δD biomarker (this study); numbers: see Supplementary Data for corresponding
412 record numbers and analyzed proxies.

413 To investigate how the EEP SST changes could have impacted the Panama Basin rainfall,
414 we updated the LGM SST anomaly compilation published in Dubois et al. (2009) with the two
415 U^{k}_{37} -based SST records of Rein et al. (2005) and Bova et al. (2015) (**Figure 6**). The resulting
416 LGM map of alkenone-based SST indicates that the gradient found between the northern
417 EPWP and the cold tongue was enhanced during the LGM compared to the Holocene
418 (Dubois et al., 2009, **Figure 6**). The magnitudes of the LGM cooling along the warm pool,
419 equatorial front and cold tongue latitudinal transect are statistically distinct (t-test, p-value <
420 0.005).

421 Over the late Pleistocene, Rincón-Martínez et al. (2010) found decreased riverine runoff
422 during glacials along the Ecuadorian margin where rainfall occurs during austral summer
423 nowadays, that were concomitant with increases in the meridional and zonal SST gradients
424 along the Equatorial Pacific. They attributed these precipitation increases to a northward
425 ITCZ shift induced by strong cooling periods along the Peruvian-Humboldt current system as
426 a whole, which acted to push the ITCZ further away from the equatorial front in the EEP
427 (Rincón-Martínez et al., 2010). In such a scenario, an increased SST gradient results in an
428 increased precipitation gradient in the EEP. This mechanism would explain why core
429 MD02-2529, situated immediately North of the modern-day precipitation maximum that
430 occurs above Panama Basin, received more rainfall in response to an ITCZ northward shift.

431 5.4.2 Ocean-atmosphere interactions in model simulations

432 We now test whether such a mechanism is at work in the PMIP4 models by considering the
433 LGM and PI simulations (Kageyama et al., 2021). The PMIP4 multi-model ensemble shows a
434 decrease in LGM precipitation in all high precipitation areas, including the EEP (see Figure 6

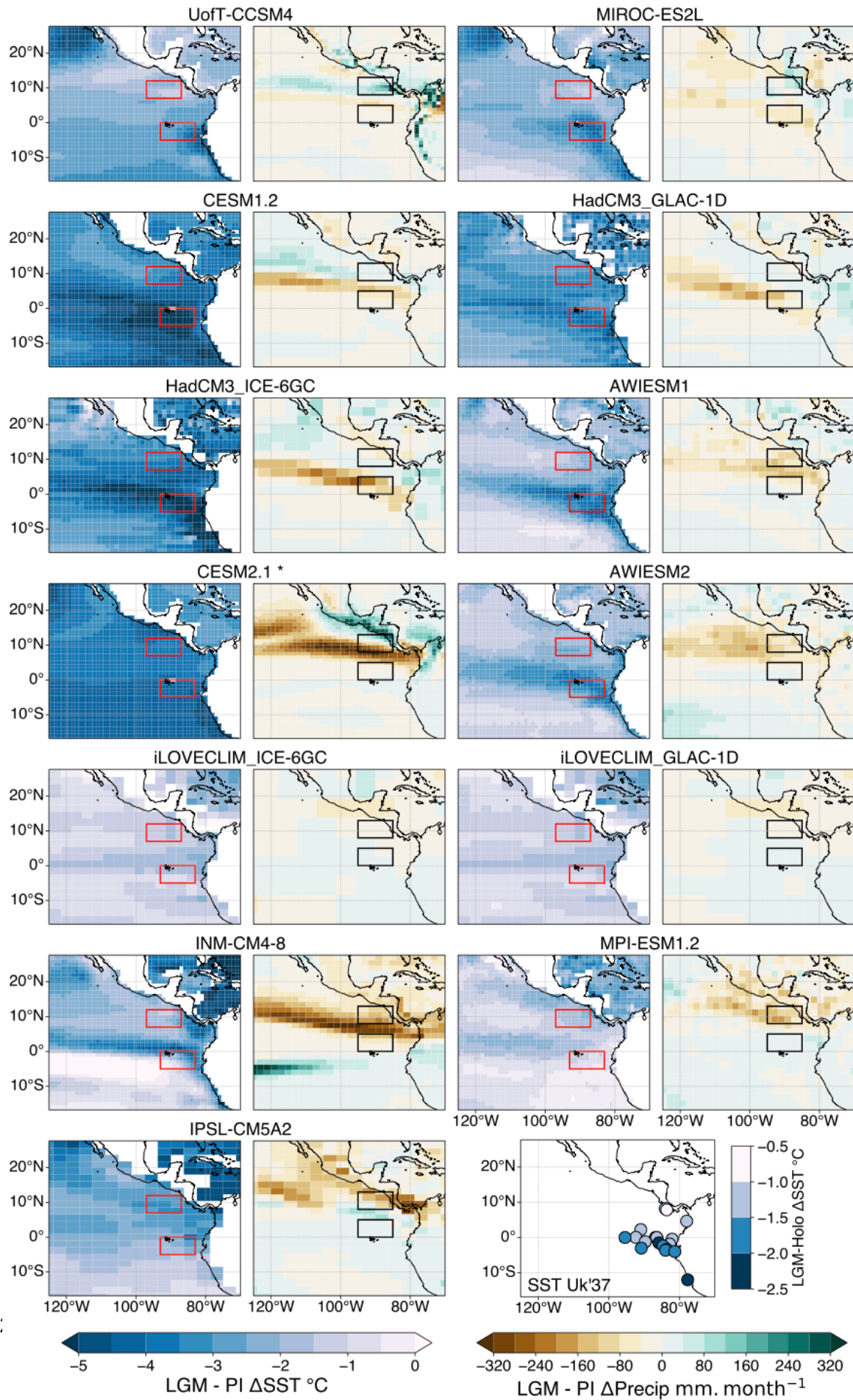
435 in Kageyama et al., 2021). However, a local response of the ITCZ induced by a regional SST
436 pattern is difficult to capture in oceanic models that already struggle to simulate the modern
437 equatorial thermocline, which also has implications for the long-standing double ITCZ bias
438 (Zhu et al., 2021b). Another source of model bias is the resolution of the orographic height in
439 different models, which changes the modelled climatology and the resulting regional SST,
440 also contributing to the double ITCZ bias in the EEP (Baldwin et al., 2021).

441 We investigate the ocean-atmosphere coupling in each individual PMIP4 LGM model output
442 to see whether, in the diversity of inter-model responses, we could detect the mechanism we
443 invoke (**Figure 6**). The set comprises thirteen LGM-PI SST and precipitation anomalies as
444 simulated by twelve models included in PMIP4 (Kageyama et al., 2021), and CESM2.1,
445 which implements the PMIP4 protocol (Zhu et al., 2021a). Based on individual models, there
446 is no agreement regarding the spatial distribution and the sign of changes in inter-model
447 precipitation anomalies (**Figure 6**). Over the thirteen models, two models exhibit a clear
448 pattern of LGM precipitation increase along the Pacific coast of Central America (CCSM4,
449 CESM2.1). Five do not really show a clear pattern (MIROC, HadCM3 ICE-6G, CESM1.2,
450 AWIESM1 and AWIESM2), with patches of slightly more or less precipitation over Central
451 America. The remaining six models (HadCM3 GLAC-1D, INM-CM4-8, iLOVECLIM GLAC-1D,
452 iLOVECLIM ICE-6G, MPI-ESM1.2 and IPSL-CM5A2) show mainly an LGM drying anomaly.
453 For most of the models though, when the LGM SST is marked by a pronounced regional
454 cooling along the equator, there is a decrease in precipitation in the immediate northern
455 vicinity of the cold tongue (**Figure 6**), suggesting that despite a vast range of regional rainfall
456 patterns for the LGM, similar ocean-atmosphere interactions were at play.

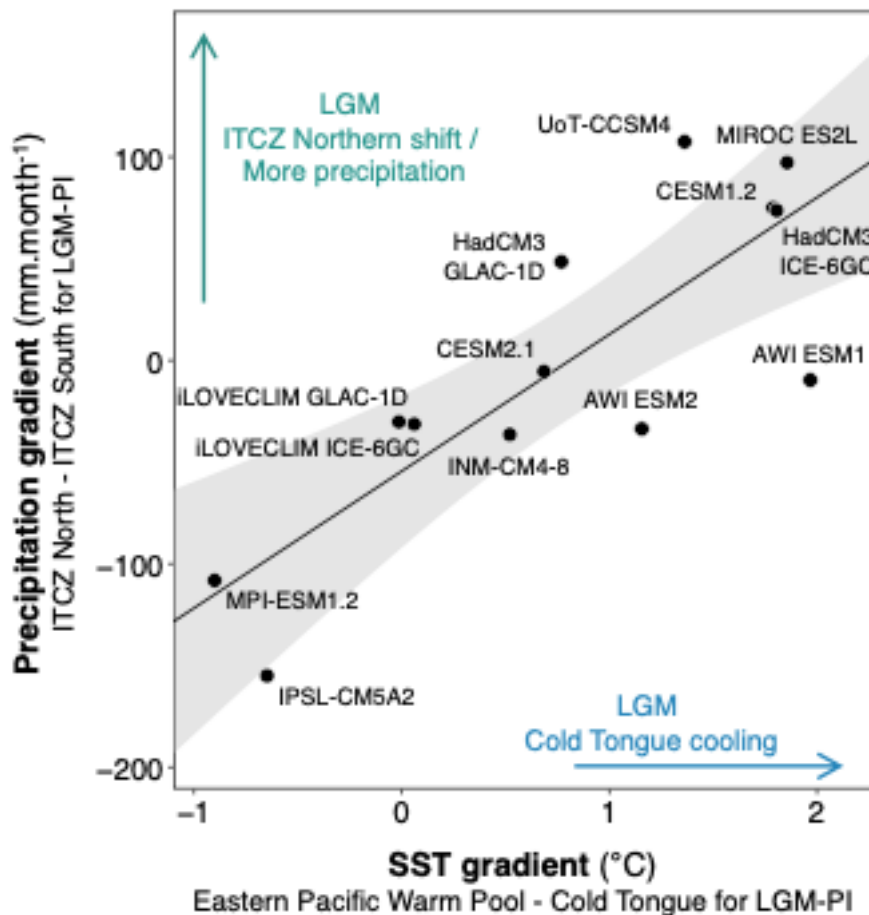
457 Regional air-sea interactions of an air parcel blowing north across the cold tongue frontal
458 zone explain that the specific humidity in the frontal region just north of the cold tongue is
459 relatively dry (Thum et al., 2002). As this northward-moving dry air parcel warms with a lag
460 relative to the underlying SST, it eventually becomes laden with moisture further north, and

461 latent heat transport occurs where the wind blows above the EPWP, i.e. north of the dry
462 region (Thum et al., 2002). Once waterlogged, the air parcel initiates intense precipitation
463 during the boreal summer when it reaches the ITCZ (**Figure 1e**, see also **Figure S2** for wind
464 vectors).

465 The SST and precipitation differences between the LGM and PI (see Methods and **Figure 6**
466 for calculation) show that there is a significant positive linear relationship between the SST
467 gradient between the EPWP and the cold tongue and the precipitation gradient between a
468 north ITCZ position and a south ITCZ position (**Figure 7**). In particular, models that simulate
469 the strong LGM cooling in the cold tongue (i.e. high SST gradient) are those that correctly
470 simulate an intensification of precipitation in the vicinity of the MD02-2529 core (**Figure 7**).
471 Models that instead simulate no LGM cooling (or even LGM warming) in the cold tongue (i.e.
472 low SST gradient) are those that simulate a decrease in precipitation (**Figure 7**). This
473 mechanism illustrates the regional influence of SST on the ITCZ.



475 **Figure 6.** LGM - PI anomalies of summer (July, August, September) SST ($^{\circ}\text{C}$) and
 476 precipitation ($\text{mm}\cdot\text{month}^{-1}$), as simulated by PMIP4 models (described in Kageyama et al.,
 477 2021 and Zhu et al., 2021a for CESM2.1). Note that SST anomalies are divided by 2 for
 478 CESM2.1 to avoid color saturation since there is an SST cooling bias reported in the model
 479 (Zhu et al., 2021a). Rectangles represent the delimited area used for SST (red) and
 480 precipitation (black) gradient calculation in **Figure 7**. The last bottom right panel shows
 481 U^k_{37} -based SST LGM-Holocene anomalies compilation from Dubois et al. 2009, updated with
 482 two U^k_{37} -based SST records (Rein et al., 2005; Bova et al., 2015). Note that the grid size
 483 shows the accurate resolution and the high spatial disparity between the models.



484

485 **Figure 7.** Correlation between the EEP ΔSST gradient (between the cold tongue and the
 486 warm pool for the LGM in comparison to the PI, red rectangles **Figure 6**) and the

487 EEP/Central America Δ Precipitation (between the precipitation area of the Northern position
488 of the ITCZ and Southern position of the ITCZ for the LGM in comparison to the PI, black
489 rectangles, **Figure 6**). 12 PMIP4 models (Kageyama et al., 2021) are plotted along with
490 CESM2.1 (Zhu et al., 2021a). Black line represents the linear regression and the grey area
491 represents the 95% confidence interval on the regression ($R^2=0.6794$, $p\text{-value}=0.0005289$).
492 Values were extracted and averaged for summer (July, August, September) in a 10° longitude
493 x 5° latitude area (red and black rectangles in **Figure 6**, refer to Supplementary Data for
494 extracted values).

495 **6 Conclusion**

496 We used δD of *n*-alkanes extracted from the MD02-2529 marine sediment core to infer
497 precipitation changes above southern Central America during the last 56 kyr. We report a wet
498 LGM co-occurring with an intensified cold-tongue cooling, suggesting that the southern
499 Central America rainfall changes intimately co-vary with the SST equatorial cold front
500 strength in the EEP. Following the LGM, we report on a progressive drying trend towards the
501 Holocene occurring during the H1. The drying trend recorded during the H1 event is
502 consistent with the regional and global hydroclimate response to a southern shift of the ITCZ.
503 However, the temporal complexity of the regional hydroclimate response to the H1 still
504 requires further study.

505 We use LGM PMIP4 simulations to better understand how regional EEP oceanic specificities
506 lead to wetter conditions in southern Central America. We identify a mechanism that involves
507 a tight ocean-atmosphere coupling in which the strength of the equatorial oceanic
508 temperature front directly impacts the ITCZ position, regardless of the sign of latitudinal SST
509 and precipitation gradients simulated by the individual models.

510 Furthermore, our results have implications for evaluating the models' abilities to accurately
511 reproduce past changes in low-latitude precipitation. Studies comparing multi-model

512 extracted data must exercise caution and use a regional approach to both highlight regional
513 climatic processes and overcome methodological bias arising from the diversity of model
514 resolutions. Finally, the accuracy in the representation of frontal zones along the equator in
515 paleoclimate simulations appears to be crucial to faithfully reproduce the associated pattern
516 of tropical rainfall changes. Those features need to be considered for future projections.

517 **Data availability**

518 MD02-2529 *n*-alkanes data will be uploaded to an online database. The ERA5 datasets are
519 available at <https://doi.org/10.24381/cds.6860a573>. The iTraCE datasets are available at
520 <https://www.earthsystemgrid.org/dataset/ucar.cgd.cesm4.iTRACE.html>. PMIP4 SST and
521 precipitation monthly model outputs were retrieved from the following database
522 <http://dods.lsce.ipsl.fr/pmip4/db/> maintained by Jean-Yves Peterschmitt, LSCE. This
523 database was partly created based on ESGF simulations cited in Kageyama et al., 2021. In
524 particular, the PMIP4-CMIP6 LGM and associated piControl simulations have the associated
525 DOIs: AWI-ESM-1-1-LR: <https://doi.org/10.22033/ESGF/CMIP6.9330> and
526 <https://doi.org/10.22033/ESGF/CMIP6.9335>; INM-CM4-8:
527 <https://doi.org/10.22033/ESGF/CMIP6.5075> and <https://doi.org/10.22033/ESGF/CMIP6.5080>;
528 MIROC-ES2L: <https://doi.org/10.22033/ESGF/CMIP6.5644> and
529 <https://doi.org/10.22033/ESGF/CMIP6.5710>; MPI-ESM1-2-LR:
530 <https://doi.org/10.22033/ESGF/CMIP6.6642> and <https://doi.org/10.22033/ESGF/CMIP6.6675>

531

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536 (He et al., 2021). The authors would like to thank all the modelling groups who provided the
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