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**OCEAN AND ATMOSPHERE TELECONNECTIONS MODULATE EAST TROPICAL
PACIFIC PRODUCTIVITY AT LATE TO MIDDLE PLEISTOCENE TERMINATIONS**

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23 **Abstract**

24 The modern Eastern Equatorial Pacific (EEP) is a key oceanographic region for regulating
25 the Earth's climate system, accounting for between 5–10% of global marine production
26 whilst also representing a major source of carbon dioxide efflux to the atmosphere.
27 Changes in ocean dynamics linked to the nutrient supply from the Southern Ocean have
28 been suggested to have played a dominant role in regulating EEP productivity over
29 glacial–interglacial timescales of the past 500 ka. Yet, the full extent of the climate and
30 oceanic teleconnections and the mechanisms promoting the observed increase of
31 productivity occurring at glacial terminations remain poorly understood. Here we present
32 multi-proxy, micropaleontological, geochemical and sedimentological records from the
33 easternmost EEP to infer changes in atmospheric patterns and oceanic processes
34 potentially influencing regional primary productivity over glacial-interglacial cycles of the
35 mid-late Pleistocene (~0-650 ka). These proxy data support a leading role for the north-
36 south migration of the Intertropical Convergence Zone (ITCZ) in shaping past productivity
37 variability in the EEP. Productivity increases during glacial periods and notably peaks at
38 major and "extra" glacial terminations (those occurring 1-2 precession cycles after some
39 major terminations) coincident with the inferred southernmost position of the ITCZ. The
40 comparison of our reconstructions with proxy records of climate variability suggests the
41 intensification of related extratropical atmospheric and oceanic teleconnections during
42 deglaciation events. These processes may have re-activated the supply of southern sourced
43 nutrients to the EEP, potentially contributing to enhanced productivity in the EEP and thus
44 counterbalancing the oceanic carbon dioxide outgassing at glacial terminations.

45

46 **KEYWORDS:**

47 East Equatorial Pacific, Intertropical Convergence Zone, benthic foraminifera,
48 paleoproductivity, teleconnections, Pleistocene terminations.

49

50 **HIGHLIGHTS**

- 51 • New multi-proxy record from the East Equatorial Pacific for the last 650 ka
- 52 • ITCZ latitudinal shifts drove productivity changes
- 53 • Ocean tunnelling likely contributed to increased productivity at terminations
- 54 • Tropical atmospheric changes key in deglaciations
- 55 • EEP contributes to the deglacial atmospheric carbon dioxide regulation

56

57

58 **1. Introduction**

59 The modern East Equatorial Pacific (EEP) plays an important role in climate regulation as
60 it is an important source of carbon dioxide (CO₂) to the atmosphere (Takahashi et al.,
61 2009). Yet, it accounts for 5-10% of the global oceanic primary production while
62 comprising only 9% of the ocean area (Pennington et al., 2006). Nutrients and CO₂-rich
63 waters are currently supplied to the EEP thermocline via Subantarctic Mode
64 Water (Sarmiento et al., 2003). Modern biogeochemical models suggest that Subantarctic
65 Mode Water provides a substantial fraction (30-50%) of the nutrients that reach the EEP,
66 thereby sustaining a large proportion of the export production in this area (Palter et al.,
67 2010). However, the mechanisms driving glacial to interglacial changes in the biological
68 productivity and export production in the EEP remain equivocal. The supply of
69 micronutrients (i.e., iron) have long been proposed as one of the main influences on the
70 efficiency and strength of the oceanic biological pump in the past (e.g. Murray et al.,
71 2012). Yet, a recent study have argued that variability in the atmospheric dust input (a
72 major source of iron) to the EEP was not large enough to trigger a substantial increase in
73 glacial productivity and that nutrient supply from the Southern Ocean might have played a
74 crucial role in controlling the equatorial Pacific productivity over the Late Pleistocene
75 (Winckler et al., 2016). The south to equatorial connection, through so called “oceanic

76 tunnelling” (Spero and Lea, 2002) appears to have been active in the past, in particular
77 during the last deglaciation (Martinez-Boti et al., 2015) and likely during older
78 deglaciations (Rippert et al., 2017). However, little is known about the functioning of the
79 oceanic tunnelling during other mid-late Pleistocene terminations and its influence on the
80 biological pump in the EEP and therefore global climate.

81 Furthermore, the EEP is involved in interhemispheric thermal and moisture transport
82 through changes in the mean position and strength of the Hadley circulation cells, which
83 are intimately linked to the meridional position of the Intertropical Convergence Zone
84 (ITCZ) (Schneider et al., 2014). Changes in the average position of the ITCZ are relevant
85 not only at a global scale, controlling global atmospheric reorganizations (Chiang et al.,
86 2014), but also regionally, involving changes in the position of oceanographic structures
87 such as the Costa Rica Dome (CRD). The CRD is an open-ocean upwelling system in the
88 EEP that develops seasonally off the coast of Central America (Fiedler, 2002). It has been
89 previously suggested that past changes in the intensity and location of the CRD upwelling
90 system depends on the intensity of the trade winds linked to the meridional position of the
91 ITCZ (Hofmann et al., 1981), and that such variability could influence regional
92 productivity patterns in the EEP during the last glacial cycle (Ivanova et al., 2012). It is
93 unclear to what extent atmospheric processes (e.g., ITCZ-related CRD variability), in
94 addition to oceanic processes (e.g., ocean tunnelling), might have influenced past
95 productivity patterns in the EEP during the mid to late Pleistocene.

96 Here we present a multi-proxy record to investigate the mechanisms controlling past
97 variability in productivity in the EEP at glacial-interglacial time scales. The record is
98 obtained from the Integrated Ocean Drilling Program (IODP), Expedition 344, Site U1381
99 (Hole U1381C) located off the Costa Rica margin (Figure 1). The core site is ideally
100 located to capture signals related to the past changes in the EEP productivity which might

101 have occurred either through variations in the position of the ITCZ, which controls the
102 extension and location of the CRD, and/or through fluctuations in the nutrient supply from
103 southern sourced waters. Accordingly, we use proxies providing information for the
104 quantity and quality of the organic carbon supply to the seafloor (e.g., benthic
105 foraminiferal faunal composition, planktonic foraminiferal abundance, organic carbon and
106 opal content) and sediment chemical composition (e.g., calcium carbonate and major
107 elemental content). These multi-proxy derived records allow us to investigate the
108 mechanisms controlling past variability in productivity and make inferences on the
109 contribution of atmospheric and oceanic processes at the glacial terminations throughout
110 the Middle to Late Pleistocene (the last 650 ka).

111

112 **2. Core location and oceanography**

113 The Hole U1381C (08°25.7027'N; 84°09.48'W, Harris et al., 2013, Figure 1) is located
114 ~4.5 km offshore the Osa Peninsula, on the Costa Rica margin at the southern end of the
115 East Pacific Warm Pool (Fiedler and Talley, 2006). The core site was recovered at 2065
116 meters, well above the depth of the modern sedimentary lysocline, which is established at
117 ~ 2900 meters water depth for the Panama basin (Thunell et al., 1981). At present, primary
118 production in surface waters at Site U1381 is relatively low as its location is not directly
119 influenced by the seasonal (wind-driven) upwelling or the current position of the open
120 ocean upwelling center of the CRD (Figure 1a-b). The lack of seasonal coastal (wind-
121 driven) upwelling at our site is because of the proximity to the Talamanca mountains
122 (3000-4000 m height) which favour the convergence of local wind curl patterns
123 (Pennington et al., 2006). This contrasts with the seasonal coastal upwelling processes
124 occurring south (Gulf of Panama, Panamá) and north (Gulf of Papagayo, Nicaragua) of the
125 Site U1381 (Figure 1c-d). The CRD is a “permanent” anticyclonic thermal structure flowing

126 cyclonically and is currently centred around 9°N and 90°W with a diameter ranging
127 between 100 to 900 km (Figure 1a-b). The CRD position and magnitude is related to the
128 seasonal migration of the ITCZ and associated wind stress curl patterns, and can be
129 identified by shallowing of the thermocline, which corresponds to the isotherm of 20°C
130 (Fig. 1a-b).

131

132 **3. Material and methods**

133 *3.1. Sediment samples*

134 Sediment samples from Site U1381 (Hole U1381C) were obtained during IODP
135 Expedition 344 (Harris et al., 2013). We analysed the uppermost 47 m cored depth scale
136 (CSF-B, meters below sea floor, mbsf, from U1381C 344-1H-1W 0-2 cm to 344-6H-1W
137 89-91 cm) which is characterised by a monotonous sequence of light greenish gray
138 hemipelagic silty clay (Harris et al., 2013). Two cm thick sediment samples for faunal
139 analysis samples (~10 cm³) were collected at a 10 cm spacing for the upper 20 mbsf and in
140 20 cm intervals for 20-47 mbsf. Samples for geochemical analysis (2 cm thick, ~10 cm³)
141 were typically taken immediately below intervals sampled for faunal analysis.

142

143 *3.2. Stable isotope analysis and age model development*

144 The age model of Hole U1381C is constructed by the combination of radiocarbon dates, a
145 planktonic biostratigraphic event and graphical correlation of the the benthic oxygen
146 isotopic ($\delta^{18}\text{O}$) record from Hole U1381C to the LR04 benthic foraminiferal $\delta^{18}\text{O}$ stack
147 (Lisiecki and Raymo, 2005). The age control of the upper sections (4.3 mbsf) is
148 constrained by seven accelerator mass spectrometry ¹⁴C ages on planktonic foraminifera
149 from the >150 μm (mixed species or monospecific depending on the availability of
150 individuals weighing between ~2 to 10 mg; see Supplementary Information S.I.1). The

151 accelerator mass spectrometry ages were measured at the Center for Applied Isotope
152 Studies, University of Georgia (U.S.A.) and were calibrated (2σ confidence limits) with
153 the Calib 7.0 software using the Marine13 calibration dataset (Reimer et al., 2013). The
154 oldest radiocarbon age was too old for calibration and was discarded for the age model
155 construction. The last occurrence of the planktonic foraminifera *Globigerinoides ruber*
156 (pink variety) occurring at 8.95 mbsf which corresponds to an age of ~ 127 ka (Ivanova et
157 al., 2012), was also used as a dating point (See supplementary information S.I.1). Beyond
158 the radiocarbon limits, the U1381C benthic $\delta^{18}\text{O}$ was correlated graphically to the orbitally
159 tuned LR04 benthic $\delta^{18}\text{O}$ stack record using the AnalySeries program. For this purpose, 3-
160 4 visually clean individuals of *Uvigerina auberiana* d'Orbigny were selected per sample
161 from the 250-300 μm size fraction. Stable isotope analyses were performed on a
162 ThermoFinnigan MAT 253 mass spectrometer coupled to a Kiel IV carbonate preparation
163 device at Cardiff University (UK). The spectrometer was calibrated through the
164 international standard NBS-19, and all isotopic results are reported as a per mil deviation
165 from the Vienna Pee Dee Belemnite scale (‰ VPDB). The reproducibility of the $\delta^{18}\text{O}$
166 analyses is $\pm 0.05\%$, based on replicate measurements of carbonate standards. According
167 to our age model, the studied interval covers the last ~ 650 ka. Average sedimentation rates
168 are 6.7 cm ka^{-1} , ranging from very low values of $\sim 1.6 \text{ cm ka}^{-1}$ during Marine Isotope Stage
169 (MIS) 2, MIS 4 and MIS 14 (which remain poorly resolved in our record) to high values of
170 $\sim 9 \text{ cm ka}^{-1}$ from MIS 5 through MIS 11 (See Supplementary Figure S1). The mean
171 temporal resolution of the records is 2 ka.

172

173 3.3. Foraminiferal faunal analyses

174 Benthic foraminiferal assemblages provide information about the quality, quantity and
175 sustainability of the organic carbon flux to the seafloor as well as oxygenation conditions

176 in the sediment and bottom waters (Gooday, 2003). Samples for benthic foraminifera
177 analyses were dried at 45°C, weighed and sieved to 63 µm, and then weighed again after
178 drying. The weight percent of the >63 µm fraction was calculated from dried samples (%
179 coarse fraction, CF). To investigate benthic foraminiferal assemblages, a representative
180 split of at least ~ 200 individuals (when possible) from the > 125 µm fraction was
181 identified and counted and the relative abundance (percentage) of the characteristic
182 species calculated. The abundance of benthic foraminifera (BF) was calculated from the
183 number of individuals counted in the split (or the whole sample when the abundance was
184 low) per gram of total dry weight sediment (number of benthic foraminifera >125 µm /g).
185 While a detailed analysis of the benthic foraminiferal fauna assemblage is out of the scope
186 of this study, ecological information is provided for the most characteristic species, or
187 group of species, relevant for a broad interpretation of paleoenvironmental conditions. In
188 order to describe the patterns of planktonic foraminifera abundance along the core, a split
189 of whole planktonic foraminifera from the >150 µm size fraction was counted and used to
190 calculate the abundance of planktonic individuals per gram of dry weight sediment
191 (number of planktonic foraminifera >150 µm /g).

192 *3.4. Organic and inorganic carbon, total nitrogen and opal contents*

193 Total bulk sediment samples for organic carbon and nitrogen content were dried at 45°C,
194 ground and homogenized using a zircon ball mill. The total weight percent of sedimentary
195 carbon (% C) and nitrogen (% N), as well as inorganic carbon (% C_{inorg}) and organic
196 carbon (% C_{org}) were measured using a macro elemental analyzer LECO CNS2000 at
197 CACTI (University of Vigo). The % C and % N measurements were calibrated against a
198 standard reference material (Ethylenediaminetetraacetic acid-EDTA and pure CaCO₃). The
199 detection limit was 0.02 % for % C and 0.01 % for % N, respectively, while repeat
200 analyses (n = 5) of the standards yielded precisions of ± 0.14 for % C and ± 0.3 % N

201 respectively. For the estimation of %C_{inorg} an aliquot of the homogenized sample was
202 heated at 450°C for 3 hours to remove organic carbon. The total weight percent of calcium
203 carbonate (% CaCO₃) was calculated as 8.33 x % C_{inorg}. The % C_{org} content was calculated
204 as the difference between % C and % C_{inorg}.

205 The concentration of sedimentary biogenic silica (i.e., % opal) is considered as a proxy for
206 siliceous export production (Anderson et al., 2009). Opal abundance was determined using
207 the method of Mortlock and Froelich (1989). The precision and accuracy of opal analysis
208 were monitored using replication of an in-house standard. The coefficient of variability
209 (e.g. standard deviation) is ± 0.2 %. The Si_{opal}/C_{org} (hereinafter Si/C) were calculated after
210 transformation of the biogenic silica (opal) and % C_{org} into molar ratios. The Si/C ratios are
211 used here as a proxy for the contribution of siliceous producers to non-siliceous primary
212 producers (Ragueneau et al., 2000).

213 Sedimentary mass accumulation rates are provided for geochemical and sedimentological
214 tracers to complement the information provided by relative abundance values. Mass
215 accumulation rates are calculated as the weight percentage of sedimentary component x
216 dry bulk density (g cm⁻³) x linear sedimentation rates (cm ka⁻¹). Linear sedimentation rates
217 are calculated from the tie points obtained for the construction of the age model
218 (Supplementary Table S1). Dry bulk density values are from Harris et al. (2013). Mass
219 accumulation rates range from 1 to 9 g cm⁻² ka⁻¹ and are within the range previously
220 estimated for the Panama basin (Kienast et al., 2007).

221

222 *3.5. Sediment chemical elements*

223 Sediment composition and provenance was evaluated by the quantification of elemental
224 concentrations of major elements (Ca, Ti, Al). For the analysis of chemical elements, dried
225 and ground sediments were prepared on pressed pellets and measured by X-ray

226 Fluorescence (XRF) using Mo as the X-ray source on a Siemens SRS 3000 spectrometer at
227 CACTI (University of Vigo). Reference samples (NRC MESS-3 and NRC PACS-2) were
228 analyzed and used as routine quality control samples, to assess the instrument accuracy and
229 to obtain quantitative values. Quantification was done using the Spectraplus Software
230 through the EVAL program by k-factor of proximity of reference samples. Replicate
231 measurements (n = 5) show good agreement between certified and analytical values.
232 Recovery was in general over 87% for MESS-3, whereas for PACS-2 it was nearly 100%
233 for all the studied elements. The typical absolute error for each element determination is
234 lower than 5%. The Ti was normalized to the Al content, an indicator of the
235 aluminosilicate fraction of the sediments. The Ti (unlike Fe) is less sensitive to
236 environmental redox variations and it is used here as a terrigenous proxy (Tribovillard et
237 al., 2006). The Ca content was normalized to Ti (Ca/Ti) and it is used here as an indirect
238 proxy for the carbonated versus terrigenous fraction of the sediment.

239

240 **4. Results**

241 *4.1.-Calcium carbonate related proxies*

242 As the Hole U1381C is ~850 m above the regional carbonate saturation horizon in the
243 Panama Basin (Thunell et al., 1981) it is not expected to have experienced severe
244 carbonate dissolution (López-Otálvaro et al., 2008). However, previous studies in the area
245 have identified some episodes of carbonate dissolution during the last glacial cycle
246 (Ivanova et al., 2012). In order to interpret the CaCO₃ variability at the core site and to
247 assess whether carbonate dissolution influenced the composition of benthic foraminiferal
248 assemblages, we used several independent proxies for CaCO₃ dissolution and
249 CaCO₃ production (e.g., LaMontagne et al., 1996): % CaCO₃ and mass accumulation of
250 CaCO₃, major elemental ratios (Ca/Ti), % >63 μm coarse fraction, relative abundance of

251 benthic to planktonic plus benthic foraminifera (B/P+B), % C_{org}, and the absolute
252 abundances of benthic and planktonic foraminifera (number of BF or PF/g) (Figure 2b-f).
253 The CaCO₃ record (% and mass accumulation) of Hole U1381C shows high values during
254 glacial periods (5-15%) and low values during interglacials (<5%) (Figure 2b). The %
255 CaCO₃ concentrations (and indirect proxies for sedimentary CaCO₃ content such as Ca/Ti)
256 peaks at major and so-called “extra terminations” (i.e., terminations exhibiting patterns of
257 events similar to main terminations, but occurring 1-2 precession cycles before), such as
258 Termination IIIa (TIIIa, between MIS 7c and 7d) and Termination VIIa (TVIIa, between
259 MIS 15a and 15b) (Cheng et al., 2016). Paleoproductivity related proxies; % C_{org},
260 abundance of planktonic and benthic foraminifera and % >63 μm (which is mainly
261 composed by planktonic and benthic foraminifera with occasional skeletons of diatoms and
262 radiolaria) exhibit generally high values during glacial periods and terminations and low
263 values during interglacial periods (Figure 2 c-f). The observed trends are statistically
264 supported by positive correlations (see Supplementary Table S.I.2). The relationship
265 between parameters seems to be noticeable at major and extra terminations, where there is
266 a significant correspondence with peaks in % CaCO₃ (and indirect proxies i.e., Ca/Ti,
267 Figure 2b), % >63 μm fraction (Figure 2c) benthic foraminifera absolute abundance (Figure
268 2d) and % C_{org} (Figure 2f). Benthic foraminifera generally outnumber planktonic
269 foraminifera (B/P+B > 0.5, Figure 2e) except for glacial stages, terminations and sub-
270 stages.

271 4.2.-Geochemical proxies.

272 The %C_{org} ranges from 0.2 to 2.2% (mean 1.9%) and concentrations increase at glacial
273 periods and peak at terminations (Figure 2f). The C_{org}/N values range from 4.4 to 13
274 (mean=9, see supplementary data), suggesting that the C_{org} at the core site is mainly of
275 marine provenance (Meyers, 1997). In contrast to %C_{org}, the % opal, which varies between

276 7% and 11%, shows only minor glacial-interglacial variability, (Figure 2g), but a clear
277 decrease in % opal at terminations. The Si/C, a proxy for the abundance of siliceous to
278 non-siliceous primary producers, shows higher values during interglacials than during
279 glacials, with the lowest values occurring at terminations (Figure 3g). The record of Ti/Al,
280 a proxy for the terrigenous provenance of the sediments, varies between 0.05 and 0.09
281 (Figure 3h). This variability range is comparable to other published Ti/Al records used to
282 infer terrigenous influence in marine sediments (e.g., Yarincik et al., 2000, Figure 3i). The
283 values of Ti/Al in the core U1381C show an increasing trend from interglacials to
284 terminations when ratios show the highest values (Figure 3h).

285 4.3.- Benthic foraminifera assemblages

286 The abundance of benthic foraminifera increases during glacial periods and peaks at
287 terminations (Figure 3a-b). Interglacial periods are characterized by low foraminiferal
288 numbers and the dominance of *Uvigerina peregrina* (Cushman) and *Uvigerina auberiana*
289 (d'Orbigny) together showing abundances higher than 40 % (Figure 3c) and therefore
290 grouped under the so-called “*Uvigerina* spp.”. This contrasts with the abundance pattern of
291 *Cassidulina carinata* Silvestri (Figure 3e) and secondary species *Valvulineria glabra*
292 Cushman and *Rotamorphina laevigata* (Phleger and Parker) (Figure 3f). *Cassidulina*
293 *carinata* almost disappears from the assemblage during interglacials (0-5%) but shows
294 increased concentrations and percentages (10-30%) during glacials and terminations. A
295 similar glacial-interglacial pattern is shown by *V. grabra* and *R. laevigata*. The last
296 deglacial period is characterized by a different set of species to the other terminations
297 (Figure 3d). *Bolivina interjuncta* Cushman, *Bolivina seminuda* (Cushman), *Bolivina* cf.
298 *plicata* d'Orbigny, *Epistominella pacifica* (Cushman), and *Epistominella smithi* (Steward
299 and Steward) characterize the assemblage of the last termination.

300

301 **5. Discussion**

302 *5.1. The carbonate record of Hole U1381C*

303 The factors explaining EEP CaCO₃ variability are still under debate (Winckler et al., 2016)
304 with some studies suggesting that CaCO₃ productivity is the main driver (Lyle et al., 2002)
305 and others instead proposing deep water carbonate chemistry (Sexton and Barker, 2012).
306 Separating the signals of production and dissolution in CaCO₃ related proxies is difficult
307 because both influences might have acted either concurrently or differently over time. It
308 therefore requires the use of several independent proxies for both CaCO₃ production and
309 dissolution (see section 4.1). The overall correlation between % CaCO₃ and indirect
310 proxies for paleoproductivity (% Corg, absolute abundance of benthic and planktonic
311 foraminifera) suggests that CaCO₃ production played a prime role in shaping sedimentary
312 CaCO₃ content at our EEP Site (Figure 2b-d). The strong correspondence between peaks of
313 % CaCO₃ and foraminiferal absolute abundance suggests that CaCO₃ production, rather
314 than minimum dissolution (preservation), is also the most likely cause for CaCO₃ deglacial
315 peaks at the core site. As an exception to this general relationship is a period of moderate
316 dissolution identified between ~ 20 and 110 ka. This interval is characterized by high
317 B/P+B ratios (Figure 2e) and planktonic assemblages dominated by dissolution resistant
318 species, such as *Globorotalia menardii* (see Supplementary Information, Figure S2).
319 Intense dissolution intervals are identified around the transition between maximum
320 interglacial and glacial declines of MIS 11 and MIS 5 (Figure 2; brown bars). These
321 intervals are represented by the extremely low abundance of whole shells of planktonic
322 foraminifera, low numbers of benthic foraminifera, low mass accumulation rate of the
323 coarse fraction, and depressed % CaCO₃ content. These samples might be affected by
324 dissolution and paleoenvironmental interpretation has been considered with caution.

325 Inferred peaks of organic export and CaCO₃ production occur at all seven major glacial
326 terminations (except for Termination V) and the “extra terminations”. Notably, the CaCO₃
327 accumulation and benthic foraminiferal abundance peaks exhibit comparable values at both
328 major and extra terminations (including terminations occurring during the period of mild
329 interglacials MIS13 and MIS15). The pattern described by our records at Termination V
330 differs from the other terminations in that the high % CaCO₃ values do not occur at the
331 termination but rather during mid glacial MIS 12 (Figure 2a-b, f).

332 5.2. *Paleoproductivity from benthic foraminifera: the influence of the CRD*

333 As outlined above, the productivity proxies at Site U1381C (e.g., C_{org} and benthic
334 foraminiferal abundance) at Site U1381C typically exhibit high values during glacial
335 periods and terminations and low values during interglacial periods (Figure 2a, d-f, Figure
336 3a-b). The deglacial productivity maxima are consistent with results from other studies in
337 the EEP for the last deglaciation (Ivanova et al., 2012) and older terminations (Winckler et
338 al., 2016). Benthic foraminiferal assemblages can provide additional information about the
339 potential mechanisms involved in those paleoproductivity changes over the last 650 ka.
340 The group *Uvigerina* spp. occurs in higher relative abundances during interglacial periods
341 (Figure 3c). One of the species within the group, *Uvigerina auberiana* is an infaunal
342 species considered well adapted to high fluxes of organic carbon under perennial upwelling
343 regimes and low to moderate oxygenation environments (e.g., Licari and Mackensen,
344 2005). Similar ecological preferences are considered for *U. peregrina*, for which some
345 studies also indicate its preference for refractory organic material (Morigi et al., 2001).
346 Therefore, high relative abundance of *Uvigerina* spp. during interglacials is suggested to
347 indicate relatively high to moderate, but sustained organic carbon flux to the seafloor. At
348 the same time, glacial periods and terminations (TII-TVII) are characterized by higher
349 benthic foraminifera abundances and increased numbers of *Cassidulina carinata* and

350 secondary species *Valvulineria glabra* and *Rotamorphina laevigata* (Figure 3e,f).
351 Ecological studies indicate that *C. carinata* favours the seasonal delivery of food to the
352 seafloor occurring during phytoplankton bloom events (Goineau et al., 2011) and that the
353 species of the genus *Valvulineria* (*V. bradyana*, *V. mexicana*) prefer eutrophic conditions
354 (Mojtahid et al., 2010). This allows for the interpretation of the occurrence of *C. carinata*
355 (and secondary species) as an indicator of the seasonal delivery of fresh and abundant
356 organic carbon to the seafloor (likely from phytoplankton blooms) in an overall context of
357 high productivity during glacials and terminations. This suggests that glacial-interglacial
358 changes in productivity are related to a variable influence of organic carbon supply from a
359 seasonal versus permanent source. There are at least two potential sources to consider that
360 which might have driven the seasonal productivity changes at Hole U1381C: (i) coastal
361 upwelling and (ii) the CRD upwelling system. Coastal (wind-driven) upwelling is not
362 favoured at the core site because of proximal high mountain ranges (See description of
363 core location and oceanography in Section 2); therefore, the most plausible source of a
364 seasonally variable organic carbon supply to Site U1381, during glacial periods and their
365 terminations, is the seasonal CRD open-ocean upwelling system. Thus, interglacial
366 conditions characterized by species related to sustainable organic carbon flux to the
367 seafloor, are interpreted as prevailing during a weak influence of the CRD over the study
368 site (similarly to the present conditions) in contrast to glacials and terminations, which are
369 interpreted as occurring when the influence of the CRD over the core site is at its highest
370 and the organic carbon input to the seafloor occurs seasonally. The similar composition of
371 modern benthic foraminiferal assemblages, as those described above, under the influence
372 of the CRD (9-11°N; Heinz et al., 2008) and outside its influence (4-8°N; Betancur and
373 Martinez, 2003) supports our interpretation. Recent foraminiferal assemblages under the
374 influence of the CRD show increased abundances of *Cassidulina carinata* (Heinz et al.,

375 2008) in comparison with assemblages from areas not directly affected by (or outside) the
376 influence of this open ocean upwelling system, which are dominated by *Uvigerina* species
377 (Betancur and Martinez, 2003). Following the arguments discussed above, we suggest
378 using the abundance of *Uvigerina* spp. group as an indirect proxy for the relative influence
379 of the CRD at Hole U1381C, with increased (decreased) abundance of these species being
380 related to distal (proximal) influence of the CRD (Figure 3c).

381 The suggestion of increased influence of the CRD over the core site during glacials and
382 terminations is also consistent with the record of sedimentary Si/C ratios (Figure 3g). The
383 CRD is a unique open ocean upwelling system as, in contrast to other upwelling systems
384 where productivity is dominated by large size diatoms, productivity is governed by
385 cyanobacteria of the *Synechococcus* group (Krause et al., 2016 and references therein).
386 Consequently, the contribution of diatoms to the organic matter export is low (Krause et
387 al., 2016). Therefore, low sedimentary Si/C ratios are expected when the CRD is close to
388 the Site U1381. Indeed, Si/C ratios are low during glacials and reach their lowest values
389 coincident with terminations (Figure 3g) further supporting the interpretation of changes in
390 the position of the CRD based on the benthic foraminiferal assemblages.

391 The foraminiferal assemblages characterizing the last deglacial period and the early
392 Holocene suggest the occurrence of intermediate to strong oxygen depletion in the bottom
393 waters, based on the known tolerance of *Bolivina interjuncta*, *Bolivina seminuda*, *Bolivina*
394 cf. *plicata* and *Epistominella smithi* and *E. pacifica* for hypoxic conditions (Silva et al.,
395 1996) (Figure 3e). Intermediate hypoxic conditions in the bottom waters are likely the
396 result of a combination of physical (i.e., reduced oxygen ocean solubility, water
397 stratification and warming) and biological processes (Tetard et al., 2017 and references
398 therein) including the excess of organic carbon supply to the sea floor delivered from
399 enhanced productivity under the influence of the CRD. The latter is supported by low Si/C

400 ratios. A similar hypoxic deglacial event has been also described in areas to the north of
401 our location such as Baja California and Santa Barbara basin (Tetard et al., 2017).

402

403

404 5.3.-Atmospheric control on the local oceanography

405 In the modern ocean, the trajectory of the CRD varies seasonally with the position of the
406 ITCZ (Fiedler, 2002, Figure 1). Thus, change in the CRD position to be more (less)
407 frequently over the site during glacial intervals and terminations (interglacials) requires a
408 southward (northward, similar to nowadays) shift in the relative position of the ITCZ.
409 Additionally, a northern (southern) position of the ITCZ would lead to increased
410 (decreased) precipitation in the EEP (Chiang et al., 2014). Hence, an increased influence of
411 the CRD over our site should parallel evidence for decreased precipitation and fluvial
412 input. The influence of freshwater inputs to Site U1381 can be assessed from the relative
413 influence of the detrital signal recorded in the elemental ratios Ti/Al (Figure 3h). The
414 variations in the Ti/Al ratios are interpreted to be driven by changes in the terrestrial run
415 off with low (high) ratios indicating more (less) run off (Yarincik et al., 2000). There is an
416 overall clear relation between low relative abundance of the *Uvigerina* spp. group
417 interpreted as increased influence of the CRD over the site (southern position of the ITCZ),
418 with high Ti/Al values indicating low terrestrial runoff. This correspondence, together with
419 other available proxies for the migration of the ITCZ in the tropical Atlantic (i.e., Ti/Al
420 record from the Cariaco Basin (Figure 3i, Yarincik et al., 2000), strongly supports the
421 suggestion that Hole U1381C is primarily recording the relative position of the ITCZ and
422 its influence on the regional hydrography of the EEP. This interpretation is further
423 supported by the similarity of the U1381C Ti/Al record and foraminiferal patterns during

424 terminations to the $\Delta\delta^{18}\text{O}$ record from Chinese speleothems (Figure 4e). The speleothem
425 $\delta^{18}\text{O}$ record is interpreted to represent abrupt changes in the precipitation regime in Central
426 Asia related to the seasonal shifts in the ITCZ position that influences the strength of the
427 Asian Monsoon (Cheng et al., 2016). When the ITCZ is displaced northward (southward)
428 the northern hemisphere summer monsoon strengthens (weakens), increasing precipitation
429 and yielding lower (higher) speleothem $\delta^{18}\text{O}$ values (higher $\Delta\delta^{18}\text{O}$, Figure 4e). The
430 correspondence between the southernmost position on the ITCZ recorded in U1381C and
431 the weakening of the Asian monsoon supports previous suggestions that such ITCZ shifts
432 are coherent over long distances (Schneider et al., 2014). Notably, our data extends
433 previous inferences from marine records (Jacobel et al., 2016) for the southward migration
434 of the ITCZ during the last two glacial terminations, indicating that comparable latitudinal
435 ITCZ variability likely characterised earlier terminations as well, such as TIV, TV, TVI,
436 TVII and the extra terminations TIIIa, TVIIa. This finding reinforces the idea that tropical
437 atmospheric changes play an essential role in the deglaciation process (Denton et al.,
438 2010).

439 *5.4.- Potential contribution of extra-tropical waters to EEP productivity during* 440 *terminations*

441 The deglacial productivity maxima observed at U1381C are related to the southward
442 migration of the ITCZ. This tropical atmospheric shift is relevant for interhemispheric
443 oceanic and atmospheric connectivity, which play a role in the increase of productivity at
444 terminations in the EEP. Thus, the inferred southward shifts in the ITCZ are coincident
445 (within age model uncertainties of $\sim 4\text{ka}$) with evidence for the delivery of ice-rafted
446 debris (IRD) to the high latitude North Atlantic sediments (Figure 4f), an indirect proxy for
447 perturbations in the Atlantic Meridional Overturning Circulation (e.g., Barker et al., 2015).
448 This linkage can be explained by atmospheric teleconnections which are reproduced in

449 coupled ocean-atmosphere models showing that large reductions in the Atlantic Meridional
450 Overturning Circulation can induce a southward shift in the ITCZ over the Pacific (Chiang
451 et al., 2014). Climate models indicate that a southward migration of the ITCZ during
452 Atlantic Meridional Overturning slowdown in the Northern Hemisphere could also cause a
453 southward shift and intensification of the Southern Hemisphere westerlies (Ceppi et al.,
454 2013). A southward displacement of the southern hemisphere westerlies would have
455 contributed to warming the Southern Ocean and Antarctica (Denton et al., 2010). Besides,
456 a weak mode of the Atlantic Meridional Overturning Circulation triggers a heat transport
457 to the Southern Hemisphere, also warming the Southern Ocean and Antarctic continent via
458 the thermal bipolar seesaw (Stocker and Johnsen, 2003). Ocean warming (i.e., retrieval of
459 glacial ice) and the shift in the Southern Ocean wind pattern would have favoured the
460 upwelling of nutrient rich deep waters in the Antarctic sector of the Southern Ocean, as
461 inferred from marine sedimentary records (Anderson et al., 2009; Jaccard et al., 2013). The
462 nutrient and carbon laden southern waters would also have advected northward, via
463 Subantarctic Mode Water (Spero and Lea, 2002), and upwelled at the EEP providing extra
464 nutrients to the equatorial thermocline, promoting primary production during the last
465 deglaciation and possibly at older terminations (Winckler et al., 2016). The effective
466 transfer of nutrients northwards is also conditioned by nutrient utilization in the Southern
467 Ocean. Low nutrient utilization in the Antarctic Sector during deglaciations, caused by low
468 iron fluxes to the Southern Ocean (Jaccard et al., 2013), implies a large proportion of
469 nutrients being transported to low latitudes. The discussed ocean and atmospheric
470 teleconnections set a favourable scenario for an active connection between Southern Ocean
471 and Equatorial waters during deglacial periods as suggested by other authors for the last
472 two glacial cycles (Rippert et al., 2017). The correspondence between the peaks in
473 productivity during glacial terminations at the core site and the abrupt rise in productivity in

474 the Antarctic sector of the Southern Ocean (ODP 1094, Ba/Fe, Jaccard et al., 2013)
475 suggests an intensification of the ocean tunnelling and an additional supply of nutrients
476 from the Southern Ocean to the U1381C site. This supply of nutrients could have
477 contributed to the increase in the productivity occurring at terminations in the easternmost
478 part of the EEP.

479 The data and interpretation discussed in this study provide a strong case for the
480 contribution of the EEP to the regulation of past ocean-atmosphere exchange of CO₂. The
481 intensification of the ocean tunnelling during terminations, evidenced by interhemispheric
482 productivity patterns, would have brought up CO₂ rich waters to the surface of the EEP
483 potentially contributing to the increase of the CO₂ atmospheric pool (e.g., Martinez-Boti et
484 al., 2015). However, a portion of this carbon would be taken up and exported by the
485 biological pump at the EEP, counterbalancing this oceanic CO₂ outgassing by transferring
486 carbon to the EEP interior. Although the net ocean-atmosphere flux at the tropical Pacific
487 over Middle to Late Pleistocene is yet unknown, the increase of productivity at
488 terminations might have acted to dampen the global atmospheric CO₂ increase occurring at
489 terminations (Bereiter et al., 2015). The described pattern might be applicable to other
490 tropical areas where the injection of southern sourced nutrients to low latitude Atlantic has
491 been interpreted to increase the productivity during the last deglaciation (Poggemann et al.,
492 2017).

493

494 **6.-Conclusions**

495 In this study, we obtained a multiproxy data set of independent proxies (geochemical,
496 micropaleoecological, sedimentological) that provide progress in our understanding of the
497 mechanisms promoting productivity changes within the easternmost part of EEP region.
498 We infer that the main processes promoting the increase of productivity in the EEP at

499 major and extra terminations over the last 650 ka is the shift of the ITCZ to a more
500 southerly position (increased influence of the high productivity upwelling centre of the
501 CRD) together with additional nutrient dvection from the Southern Ocean. From these
502 arguments we infer that both interhemispheric oceanic and atmospheric mechanisms were
503 involved in the productivity increase at terminations at the EEP. This deglacial
504 productivity increase potentially played a role in the glacial-interglacial atmospheric CO₂
505 regulation by dampening the deglacial rise in atmospheric CO₂. The new data presented
506 here suggest that the EEP is a key region in climate regulation playing a role in the global
507 atmospheric and ocean reorganizations occurring at Middle to Late Pleistocene
508 terminations.

509

510 **Data availability:** Data presented in this manuscript are provided in an excel file, Data.xls.

511

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690 **FIGURES AND FIGURE CAPTIONS**

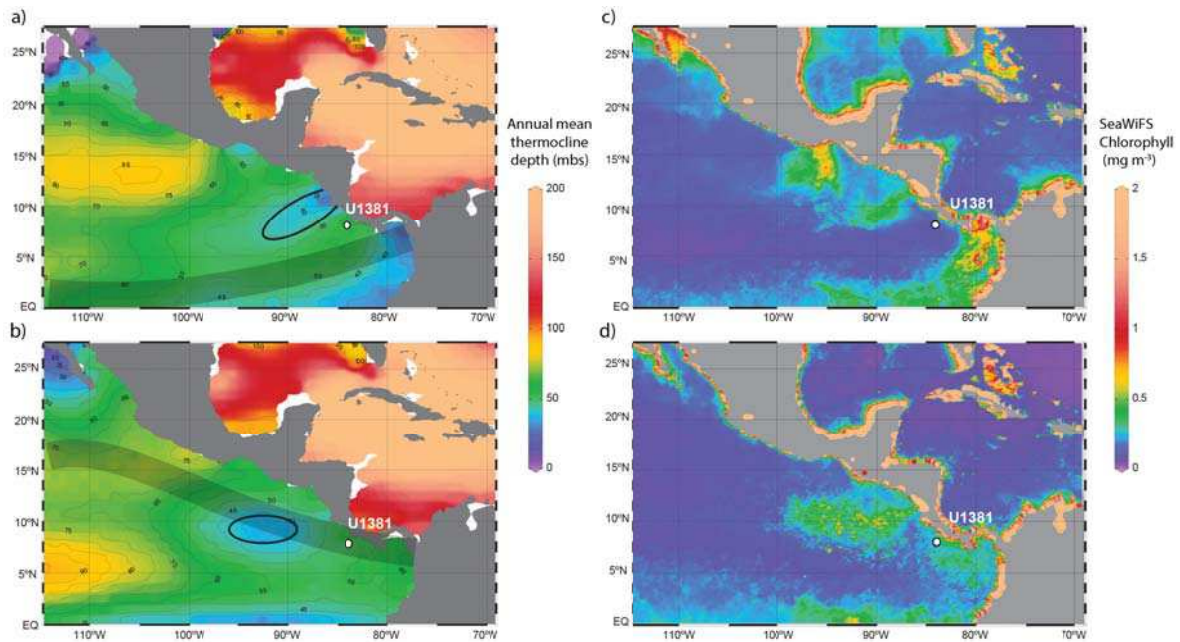
691

692 **Figure 1: Location of Hole U1381C and regional hydrography**

693 Figures on the left (a, b) represent the seasonal (winter above; summer below) depth (in
694 meters below surface, mbs) of the 20°C isotherm in region of the EEP, which is used to
695 identify the position of the Costa Rica Dome (Fiedler, 2002). The shadowed area
696 represents the position of the ITCZ in winter (a) and summer (b). Thermocline temperature
697 data are from World Ocean Database 2013 (Locarnini et al., 2013). The white circle
698 indicates the location of Hole U1381C. Plots on the right (c, d) represents the winter (c)
699 and summer (d) mean fields of SeaWiFS (September 1997 to July 2001) chlorophyll
700 concentration in the region of the Costa Rica Dome. SeaWiFS data produced by NASA
701 SeaWiFS Project and distributed by the Distributed Active Archive Center at
702 NASA/Goddard Space Flight Center (<http://oceancolor.gsfc.nasa.gov>, accessed on 1st
703 February 2018).

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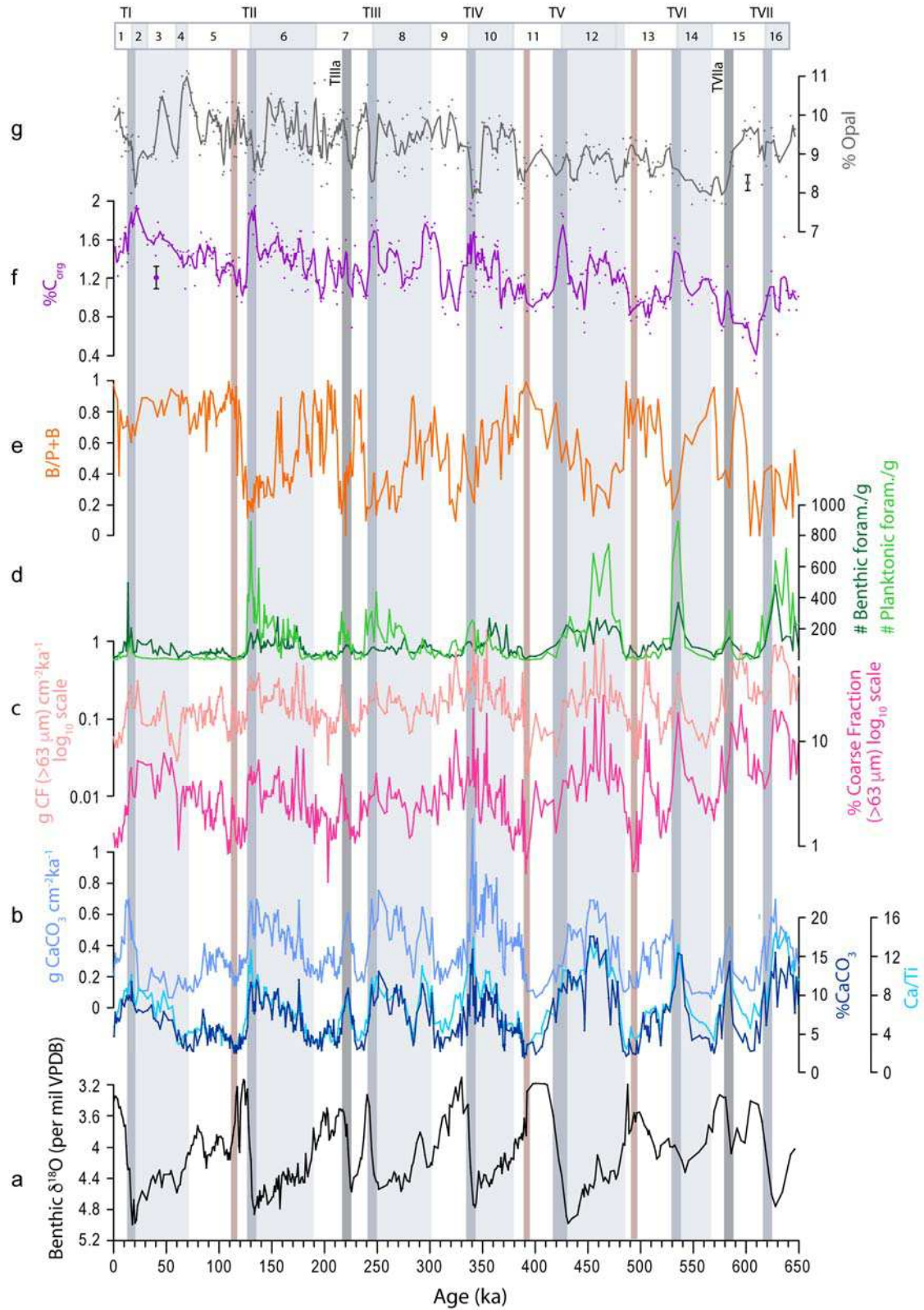
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708 **Figure 2: Calcium carbonate variability.**

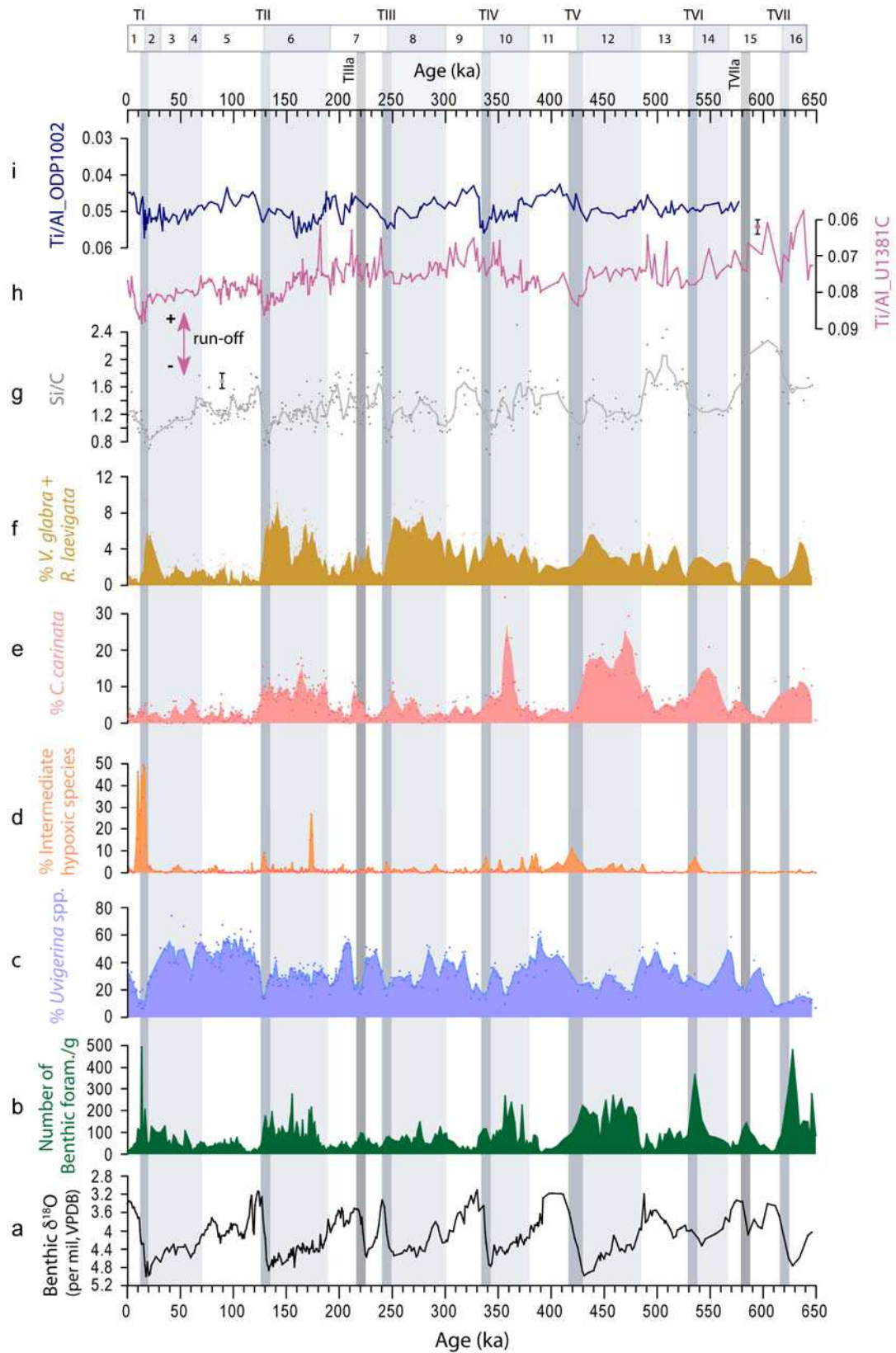
723 The benthic oxygen isotope record of *Uvigerina auberiana* (a) and carbonate records (b) of
 724 Hole U1381C are compared with other proxies for carbonate dissolution/production
 725 obtained in the same core (c-g). (b) % CaCO_3 and Ca/Ti (right axis) and mass CaCO_3
 726 accumulation rate (left axis); (c) percent (right) and mass accumulation (left) of the coarse
 727 fraction (>63 μm); (d) abundance of benthic foraminifera (number of benthic
 728 foraminifera >125 μm fraction per gram of dry weight sediment) and planktonic
 729 foraminifera (number of planktonic foraminifera >150 μm fraction per gram of dry weight
 730 sediment). The relation of benthic foraminifera to planktonic and benthic foraminifera
 731 (B/P+B) is indicated in (e). The organic carbon content of the core is used as a proxy for
 732 organic production (f) and complements the information provided by benthic foraminifera
 733 (d). The opal content (%) is indicated in (g). Lines for the content of C_{org} (f) and %opal (g)
 734 represent the 3-points running average. Vertical bars to the side of plots (f) and (g) indicate
 735 standard error of C_{org} ($\pm 0.14\%$) and opal ($\pm 0.2\%$) analyses. Vertical grey bars indicate
 736 glacial periods (light grey) and major terminations (dark grey) and “extra terminations”
 737 (very dark grey). Brown vertical bars indicate potentially heavily dissolved intervals.



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724 **Figure 3: Benthic foraminiferal assemblages**

725 The benthic $\delta^{18}\text{O}$ curve and the abundance of benthic foraminifera (number of benthic
726 foraminifera >125 μm per gram of dry weight sediment) are shown for reference in (a) and
727 (b). The records of the most characteristic species of benthic foraminifera in Hole U1381C
728 expressed in percentage are indicated in (c-f). Filled areas represent the 3-point running
729 average. The Si/C ratio (g, 3-point running average) is used here as a proxy for the
730 abundance of siliceous to non-siliceous primary producers. The Ti/Al record in the Hole
731 U1381C is plotted on inverted axis on the right (h) and the record of Ti/Al of ODP-1002
732 on the left (Yarincik et al., 2000) (i). The Ti/Al records indicate decreased (increased)
733 runoff - high (low) Ti/Al ratios- which are related to the relative movement of the
734 terrestrial ITCZ with high (low) ratios corresponding to a southerly (northerly)-most
735 position of the ITCZ. The average error of Ti/Al and Si/C measurements is indicated by
736 vertical bars to the side of plots (g) and (h). The *Uvigerina* spp. group includes *Uvigerina*
737 *auberiana* and *Uvigerina peregrina*. The group of the so called intermediate hypoxic
738 species includes *Bolivina interjuncta*, *Bolivina seminuda*, *Bolivina* cf. *plicata*,
739 *Epistominella pacifica* and *Epistominella smithi*. Vertical grey bars are as indicated in
740 Figure 2.



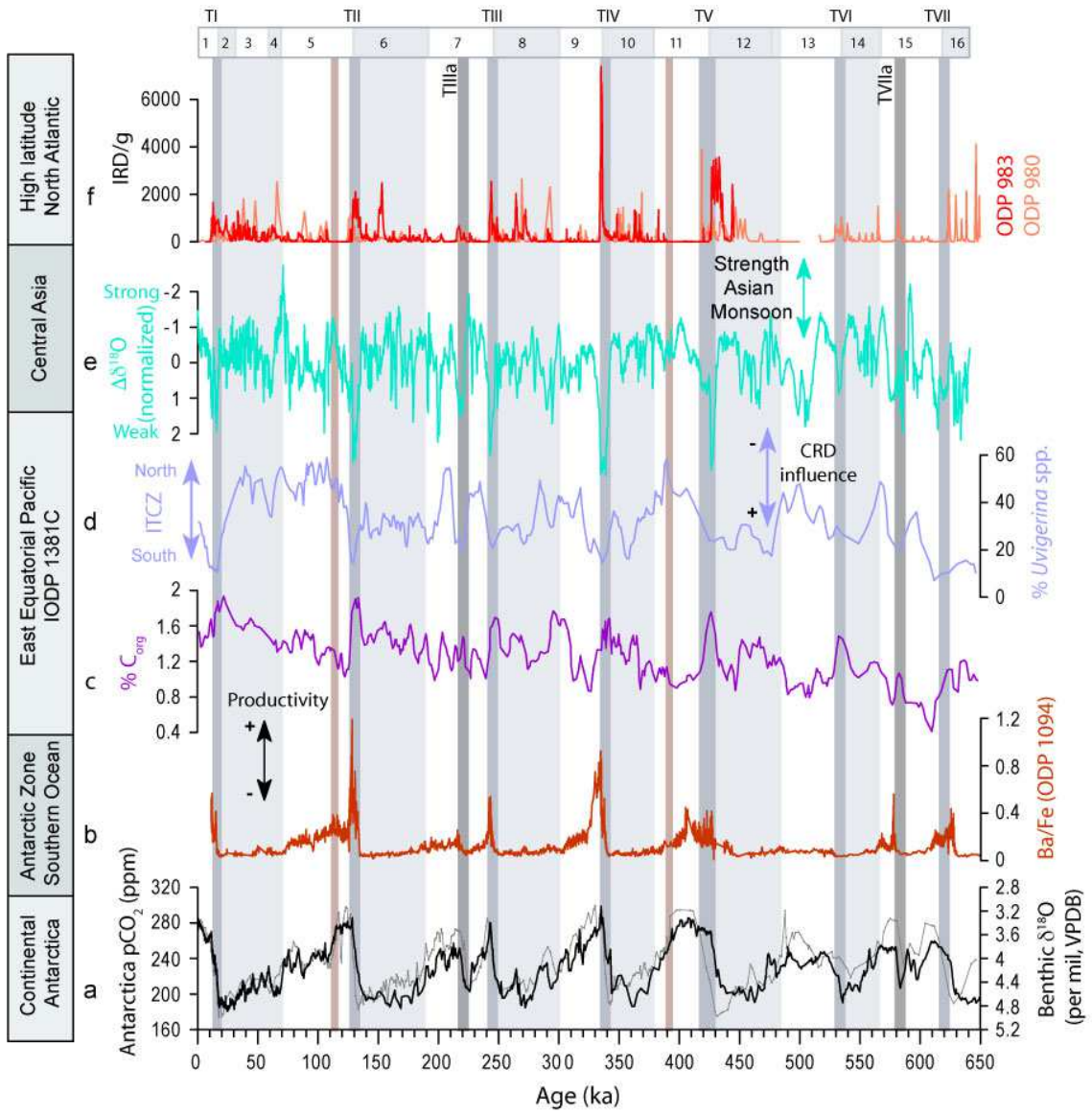
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744 **Figure 4: Atmospheric and oceanic interplay at terminations.**

745 Proxies for the Antarctic Continent (a), the Antarctic sector of the Southern Ocean (b) are
746 compared to proxies obtained in the EEP (c-d; Hole U1381C, this study), central Asia (e)
747 and the high latitude North Atlantic (f). The oxygen isotope record of Hole U1381C (a,
748 grey) is plotted to the right of the Antarctic CO₂ composite (Bereiter et al., 2015). The
749 productivity record of the Antarctic sector of the Southern Ocean (b) is represented by the
750 Ba/Fe record of ODP Site 1094 (Jaccard et al., 2013) and is compared to Hole U1381C
751 records of (c) %C_{org} as a proxy for productivity and (d) the percentage of *Uvigerina* spp.
752 group, which is related to the influence of the Costa Rica Dome and therefore, a proxy for
753 the relative position of the ITCZ. The increased (decreased) abundance of *Uvigerina* spp.
754 is related to the northward (southward) position of the ITCZ. Data from this study lead to
755 the suggestion that the southernmost position of the ITCZ in the EEP is attained at
756 terminations (both major and extra terminations) in close correspondence with abrupt
757 weakening of the Asian Monsoon (e). The record of $\Delta\delta^{18}\text{O}$ (e) from Chinese caves
758 represents a cave composite $\delta^{18}\text{O}$ signal obtained after removing the orbital insolation
759 component (Cheng et al., 2016). Records of Ice Rafted Detritus (IRD, number/g) in the
760 high latitude North Atlantic (ODP Site 983 data from Barker et al., 2015, redline; ODP Site
761 980 data from McManus et al., 1999 and Wright and Flower, 2002, orange line) are
762 indicated in (f). Note that age models are plotted on their published age scales; ODP Sites
763 983 and 1094 are tuned to ice core records whereas Hole U1381C and ODP Site 980 are
764 tuned to an orbital stack. Vertical bars are as indicated in Figure 2.



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