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Speleothem record attests to stable environmental conditions during Neanderthal-modern human turnover in southern Italy

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1 **Speleothem record attests stable environmental conditions during**
2 **Neanderthal-Modern Human turnover in Southern Italy**

3

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20

21 **The causes of Neanderthal-Modern Human (MH) turnover are ambiguous.**
22 **While potential biocultural interactions between the two groups are still**
23 **little known, it is clear that Neanderthals in southern Europe disappeared**
24 **about 42,000 years ago (ka), after ~3,000 years long cohabitation with MH.**
25 **Among a plethora of hypotheses on Neanderthal extinction, rapid climate**
26 **changes during the Middle to Upper Palaeolithic transition (MUPT) are**
27 **regarded as a primary factor. Here we show evidence for stable climate and**
28 **environmental conditions during the MUPT in a region (Apulia) where**
29 **Neanderthals and MH coexisted. We base our findings on a rare last glacial**
30 **stalagmite deposited between ~106 and ~27 ka, providing the first**
31 **continuous western Mediterranean speleothem palaeoclimate archive for**
32 **this period. The uninterrupted growth of the stalagmite attests the**
33 **constant availability of rainfall and vegetated soils, while its $\delta^{13}\text{C}$ - $\delta^{18}\text{O}$**

34 **palaeoclimate proxies demonstrate that Apulia was not affected by**
35 **dramatic climate oscillations during the MUPT. Our results imply that**
36 **climate did not play a key role in the disappearance of the Neanderthals in**
37 **this area, thus the Neanderthal-MH turnover must be approached from a**
38 **perspective that takes into account climate and environmental conditions**
39 **favourable for both species.**

40

41 **Background**

42 There is no leading theory about the triggers of the most important cultural
43 transition in human history^{1,2}. Rapid climate shifts during the MUPT are
44 considered as one of the most important drivers of the Neanderthal-MH
45 interchange²⁻⁸, because of the impact on population/depopulation dynamics^{7,8},
46 fragmentation of optimal habitats⁶, deterioration of environmental conditions³,
47 and/or the weakening of local communities after severe cold and dry stages⁴.
48 Accordingly, the Neanderthals have been inexorably afflicted by recurrent
49 millennial- to centennial-scale dry and cold conditions attributable to
50 Dansgaard–Oeschger (DO) cycles and especially Heinrich (H) events during
51 Marine Isotope Stage (MIS) 3. H events induced aridity and cold temperatures in
52 Western and Central Europe¹⁰, and those occurring from ~63 to ~40.5 ka (H6 to
53 H4) had irreversible impacts on the Neanderthal population⁵. The one at ~40.5
54 ka (H4) caused the final Neanderthals' demise and/or their migration into other
55 areas where the extinction occurred later². However, this is at odds with the fact
56 that H events lack consistent equivalents in the Mediterranean realm¹¹ and they
57 may have not necessarily resulted in very harsh climate conditions in the entire
58 region¹². Additionally, Neanderthal extinction might have occurred before H4¹³.
59 Indeed, there are chronological and spatial impediments in solving this
60 conundrum, because of age uncertainties of both the palaeoclimate and the
61 anthropological events, and the unknown response of local Neanderthal-MH
62 habitats to high-latitude driven climate change. Moreover, ancient human
63 communities occupied only small portions of land with ideal settlement
64 conditions, and the gradual climate deterioration of the last glacial period likely
65 reduced the extent of these optimal Neanderthal habitats⁶. The 2,600 to 5,400
66 years-long interval of Neanderthal-MH coexistence was likely unevenly

67 distributed in space¹³. Therefore, climate-related hypotheses should be based on
68 records from the same area where Neanderthals-MH actually cohabitated, but
69 these records are scarce¹⁴.

70 Neanderthal and MH remains are widespread from northern to southern Italy⁹.
71 This study targets Apulia (Fig. 1), where Neanderthals were present since at
72 least MIS 5e until ~42 ka, while the earliest European MH appeared in this
73 region ~45 ka^{1,9}. Thus, this is a strategic region for understanding the biocultural
74 processes occurring during the Neanderthal-MH transition and, ultimately,
75 whether climate played a decisive role in the disappearance of the former and in
76 the territorial supremacy of the latter.

77

78 **Results**

79 We explored several caves in Apulia searching for speleothems (Extended Data
80 Figure 1). Uranium-thorium (U-Th) radiometric dating on 14 stalagmites
81 (Extended Data Figure 5 and Supplementary Table 1) attests that cave calcite
82 deposition was abundant during the last and older glacial periods (Fig. 1). Here
83 we focus on stalagmite PC from Pozzo Cucù Cave (40.90° N, 17.16° E), for which
84 27 stratigraphically aligned U-Th dates (Supplementary Table 1) were used to
85 produce an age-depth model (Extended Data Figure 6). Accordingly, PC grew
86 uninterruptedly from 106.0 ^{+2.8}/_{-2.7} to 26.6 ^{+0.8}/_{-0.9} ka, and thus covers MIS 5 to
87 MIS 3 (Fig. 2). High-resolution $\delta^{18}\text{O}$ - $\delta^{13}\text{C}$ analyses (n = 2659) reveal a pattern
88 comparable to the North Greenland Ice Core¹⁵ (NGRIP) from the entire MIS 5 and
89 4. During MIS 3, $\delta^{18}\text{O}$ shows a less evident – but still recognisable – similarity
90 with NGRIP, while $\delta^{13}\text{C}$ yields a plateau-like signal. Importantly, $\delta^{18}\text{O}$ - $\delta^{13}\text{C}$ does
91 not show evidence of many of the most severe climate events affecting northern
92 latitudes (e.g., Heinrich events).

93

94 **Discussion**

95 Because glacial stages in the Mediterranean area were generally dry and
96 characterised by sparse vegetation, continuous speleothem growth was rare. In
97 Italy, for example, there is no evidence of uninterrupted stalagmite deposition
98 during glacial periods (Fig. 1). To our knowledge, the longest record has been
99 constructed by using four speleothems (two stalagmites and two stalactites)

100 found in Frassassi Cave¹⁶. In the Iberian Peninsula, speleothem formation was
101 also intermittent^{11,17,18}, while more continuous deposition is only known from
102 caves in Turkey and on the south-eastern side of the Mediterranean Sea^{19,20}. The
103 continuous growth of speleothems in Manot Cave (Israel) has been recently
104 taken as evidence for the lack of water shortage in northern Israel during the last
105 glacial period²¹. Considering that continuous speleothem deposition is only
106 feasible if the karst reservoir is recharged by rainfall and soil bioactivity
107 procures high amounts of CO₂ to infiltrating water, Apulia's glacial climate was
108 possibly milder than in other areas in the western and central Mediterranean.
109 The $\delta^{13}\text{C}$ values of PC are representative of soil activity^{10,11} (see methods). For
110 most of the time, values are more negative than -5.0 ‰ (Fig. 2), attesting the
111 presence of C3 plants²² that normally prevail in temperate regions.
112 It is well established that $\delta^{18}\text{O}$ in speleothems from the Mediterranean
113 principally reflects rainfall amount variations²³. Secondly, it might also record
114 changes in moisture sources²⁴. Because of the striking resemblance between PC-
115 $\delta^{18}\text{O}$ and NGRIP $\delta^{18}\text{O}$ (Fig. 2), especially during MIS 5 and 4, we are confident
116 that the stalagmite recorded the effects of climate change in the high latitudes
117 and the North Atlantic. This intrahemispheric connection is translated into
118 rainfall oscillations during DO cycles, with higher (lower) rainfall amount during
119 interstadials (stadials) as expressed by more negative (positive) $\delta^{18}\text{O}$ values.
120 This correlation can also be seen at the intra-stadial/interstadial timescale²⁵
121 (Extended Data Figure 2). Intriguingly, the shape of several MIS 5 DO-like events
122 in PC (e.g., DOs from ~90 to ~70 ka) appear more similar to the Asian monsoonal
123 oscillations²⁶ than to NGRIP (Extended Data Figure 3), a feature worth to be
124 examined in detail in future studies. Variability of PC growth rate and $[\text{}^{234}\text{U}/\text{}^{238}\text{U}]_i$
125 (Extended Data Figure 4) agrees with PC- $\delta^{18}\text{O}$ being principally driven by rainfall
126 amount (see methods). Changes in the dominant moisture source are possibly
127 reflected by the PC- $\delta^{18}\text{O}$ values too. During Greenland Interstadials (GIs) rainfall
128 in the Mediterranean region was predominantly Atlantic-sourced giving rise to
129 more negative $\delta^{18}\text{O}$ values, similar to today^{23,27}. Conversely, Mediterranean-
130 sourced moisture showing more positive $\delta^{18}\text{O}$ values prevailed when large ice
131 sheets during Greenland Stadials (GSs) impeded the Westerlies from efficiently
132 delivering moisture to the Mediterranean region (see methods). This is because

133 the lower moisture production in the Atlantic, according to the relative decrease
134 of GSs temperatures, limits advection over the Mediterranean²³. As the Atlantic
135 moisture input decreases, the ratio between Mediterranean/Atlantic moisture
136 increases in the area of study. The further expansion of northern ice-sheet since
137 MIS 3 probably caused a pronounced southward shift of the Westerlies²⁴, that
138 might have boosted this mechanism.

139 The covariation of $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ in PC is consistent with rainfall amount being a
140 primary driver (Fig. 2). In Apulia, rainfall coupled with temperature variations as
141 recorded by other archives (Fig. 3) modulated soil organic activity reflected by
142 the $\delta^{13}\text{C}$ record of PC (Fig. 2). Between DO 24 and DO 15, bioproductivity
143 increased during GIs giving rise to more negative $\delta^{13}\text{C}$ values. Because of reduced
144 rainfall and lower temperatures during GSs, bioproductivity decreased resulting
145 in more positive $\delta^{13}\text{C}$ values. The generally low $\delta^{13}\text{C}$ values in conjunction with
146 the lack of growth stops in PC strongly argues for a continuously vegetated
147 catchment of the cave's drip water with expanding forests during GIs and trees
148 becoming sparse during GSs (Fig. 3), in agreement with nearby pollen
149 records^{28,29}. The PC $\delta^{18}\text{O}$ - $\delta^{13}\text{C}$ data suggest two periods of extremely dry
150 condition, when both isotopes show peak values: from $66.7^{+0.9}/_{-1.2}$ to $65.6^{+1.1}/_{-1.3}$
151 ka during MIS 4, and from $55.3^{+1.1}/_{-2.5}$ to $54.9^{+1.1}/_{-2.7}$ ka during MIS 3. Both
152 events deviate from the NGRIP variability but agree with speleothem¹¹,
153 lacustrine²⁹ and marine records³⁰ from the Mediterranean region. They have
154 been attributed to markedly dry conditions during ice-rafting events and
155 increases of cold-water foraminifera in the North Atlantic during H events 6 and
156 5a^{11,31}. Although the aridity of these events was not sufficient to stop carbonate
157 deposition at the PC site, as occurring in speleothems from continental Europe¹⁰
158 (Fig. 3g), these periods are here regarded as the driest and probably coldest of
159 the entire MIS 5 to 3 timespan at least in Southern Italy. The event at ~ 55 ka was
160 certainly the driest of the entire record as reflected by the highest $\delta^{13}\text{C}$ values
161 and a marked reduction in growth rate (Fig. 1 and Extended Data 4). This event
162 was likely even drier than GS24 and GS23, from $105.2^{+2.4}/_{-2.3}$ to $102.4^{+2.1}/_{-2.0}$ ka
163 and from $95.7^{+0.9}/_{-0.8}$ to $93.1^{+0.7}/_{-0.9}$ ka, which also led to $\delta^{13}\text{C}$ values higher than
164 -5 ‰.

165 There is no correlation between PC- $\delta^{18}\text{O}$ and NGRIP for DO 14 and 13 (Fig. 2),
166 likely because of the low resolution due to the slow growth rate. From DO 12 to
167 the top of the record, PC shows its most interesting features: i) PC- $\delta^{18}\text{O}$ reveals
168 NGRIP-like millennial-scale oscillations, although the similarities with NGRIP are
169 strikingly less evident than prior to ~ 55 ka. The implication is that rapid climate
170 oscillation during MIS 3 recorded in Greenland had a lower impact on rainfall
171 variability in Apulia than those during MIS 5 and 4; and ii) these oscillations are
172 superimposed to a general PC- $\delta^{18}\text{O}$ trend toward more positive values (Fig. 2),
173 which is synchronous with the progressive reduction of the stalagmite's
174 diameter (Fig. 1). Considering that the latter mirrors long-lasting reduced
175 dripping and thus calcite deposition at the top of the speleothem³², these
176 observations point to a middle to upper MIS 3 in Apulia characterised by a
177 progressive rainfall reduction rather than by rapid and severe climate switches.
178 At this point the Mediterranean might have become the primary source of
179 moisture because of the expansion of the Northern ice-sheets. This is consistent
180 with a gradual increase in the $\delta^{18}\text{O}$ value of the moisture source for PC.
181 Furthermore, rainfall amount variability during MIS 3 GIs and GSs, caused by
182 Mediterranean cyclogenesis, is not comparable to that induced by a higher
183 efficiency of Westerlies delivering moisture during MIS 4 and 5. This is because
184 the availability of moisture is lower than when the Atlantic is the principal
185 moisture source. Most importantly, from ~ 55 ka onward PC $\delta^{13}\text{C}$ values show a
186 "plateau-like" feature during MIS 3 (Fig. 2). This cannot be explained by in-karst
187 processes and/or kinetic mechanisms affecting isotopic fractionation (see
188 methods), but rather reflects stable soil dynamics and only minor vegetation
189 changes. Preliminary $\delta^{18}\text{O}$ - $\delta^{13}\text{C}$ data from another Apulian stalagmite (SA1, Fig. 2
190 and Extended Data 5) agree with PC³³. This reinforces the idea that drastic
191 rainfall (and temperature) variations were minimal and insufficient to cause
192 major changes in soil bioproductivity and/or interruptions in speleothem
193 deposition. Speleothems from Frassassi cave¹⁶, the only Italian record available
194 for comparison (Fig. 1), also report \sim constant $\delta^{18}\text{O}$ - $\delta^{13}\text{C}$ (Fig. 3) from ~ 55 ka to
195 at least ~ 30 ka, which was interpreted as mirroring relatively stable climatic
196 conditions in the northeastern Apennines. The slight depletion trend that is
197 visible in the PC- $\delta^{13}\text{C}$ plateau may appear inconsistent with the gradual decrease

198 in rainfall expressed by PC- $\delta^{18}\text{O}$. We advance the possibility that the lack of
199 severe droughts, which would also cause the total/partial soil erosion, allowed
200 an enduring maturation of pedogenic layers although the general trend of
201 climate deterioration. This hypothesis will be thoroughly explored by future
202 studies. Vegetation shifts likely occurred, but they were possibly less
203 pronounced than in the nearby Monticchio Lake²⁸ area (Fig. 3) because of the
204 proximity with the coast and the lower altitude.
205 Accordingly, from ~55 ka onward we set the beginning of environmental niche
206 conditions in Apulia¹. Neanderthals settled in this region well before MIS 3, so
207 Apulia cannot be considered a *refugia*³⁴ for them. Contrarily to Apulia,
208 freshwater availability, as well as vegetation, was scarce in the northern parts of
209 the Italian Peninsula as highlighted by speleothem deposition (Fig. 1). This
210 attracted wildlife and new hunter-gatherer communities.
211 Favourable settlement conditions might have fostered the arrival of MH in Apulia
212 and their coexistence with Neanderthals (Fig. 2). The disappearance of
213 Neanderthals in Apulia (~42 ka) occurred ~13,000 years after the cold and dry
214 interval at ~55 ka, while the following H5 (~45 ka) apparently did not have a
215 strong impact on the local environment. This is confirmed by arboreal pollen
216 values above 40% in the nearby Monticchio Lake record²⁸. In contrast, pollen in
217 Greece²⁹, planktonic foraminifera in the Tyrrhenian Sea³⁰ and speleothems from
218 Iberia¹¹ and Turkey¹⁹ record climate deterioration during H5 at around 48 ka
219 (Fig. 3), further suggesting that Apulia was a favourable environmental niche
220 during MIS 3 in comparison to other localities. It has been recently shown³⁵ that
221 the climate in Morocco responded inconsistently to northern high-latitude ice-
222 rafted debris events, with even pluvial phases occurring during these cold and
223 dry periods. This calls for a re-evaluation of the role of the northern high
224 latitudes in triggering major cooling/drying events across the Mediterranean
225 region. Even supposing a late Neanderthal presence in Southern Italy, e.g. later
226 than ~42 ka, the fact that the impact of H4 (~40.5 ka) on PC's proxy data is
227 negligible further excludes climate as the major trigger for the Neanderthal-MH
228 turnover during MUPT.

229

230 **Final remarks**

231 PC represents strong evidence of environmental stability in Apulia during the
232 Neanderthal-MH turnover, hence high latitude rapid climate changes were not
233 the primary cause of Neanderthals' disappearance in this region. Opposite
234 opinions face the paradox that shifts toward a dry and cold climate did not result
235 in a cessation of speleothem deposition, but caused the extinction of a species
236 well adapted to the surrounding environment and that survived previous climate
237 periods more severe than MIS 3. Consequently, this applies to all European mid-
238 latitude regions where DO climate variations during MIS 3 were attenuated by
239 latitudinal, orographic and/or geographical factors. In all Apulia-like niches, the
240 issue of the Neanderthal-MH turnover must be approached from a perspective
241 that takes into account climate and environmental conditions favourable for
242 both species. This interestingly differs from the Levantine area where there was
243 no water shortage during MUPT, but speleothem $\delta^{13}\text{C}$ suggest an alternation
244 between woody and more open vegetation. The adaptation of different modern
245 cultures that possibly interacted with Neanderthals has been there defined as
246 landscape-dependent²¹. In Apulia-like niches instead, the advanced hunting
247 technology of MH groups over Neanderthals since their migration to Europe³⁶⁻³⁹
248 appears now a solid reason to explain the territorial supremacy of the former
249 that induced the extinction of the latter after ~3000 years of coexistence.
250

251 **Methods**

252 **Cave sampling and speleothem subsampling**

253 The caves explored for this work are: Pozzo Cucù (40.90° N, 17.16° E), Trullo
254 (40.85° N, 17.11° E), Sant'Angelo (40.73° N, 17.57° E) and Zaccaria (40.74° N,
255 17.55° E) (Extended Data Figure 1). For the conservation of the cave
256 environment, all speleothems used in this study were found displaced from their
257 original position, sometimes in multiple pieces. No hammer or any cutting tools
258 were employed during sampling. PC stalagmite was found right next to its
259 growing location. All stalagmites were cut along the central axis and polished to
260 allow a better visualization of the internal layering and macrofabrics. For U-Th
261 dating, ~100 mg calcite powders and/or chips were obtained by milling along a
262 discrete number of growth layers. Drill bits of 1 mm and 0.8 mm were used for
263 preliminary and detailed dating, respectively. For stable isotope subsampling,
264 one half of PC was quartered, in order to precisely conduct milling operation
265 along the central axis. The milling increment was 0.1 mm between the top and 51
266 mm from the top, and 0.2 mm from 51 mm to the bottom of the stalagmite. A
267 total of 2659 subsamples was obtained. See Fig. 1 for subsampling location. The
268 milling resulted in an average resolution of ~30 yr (range ~20 to 175 yr).

269

270 **U-Th dating and $\delta^{13}\text{C}$ - $\delta^{18}\text{O}$ analyses**

271 The majority of U-Th dating was accomplished at the University of Melbourne
272 (Australia), School of Earth Sciences, while a minor part was carried out at the
273 Xi'an Jiaotong University (China), Institute of Global Environmental Change
274 (Supplementary Table 1). In Melbourne, ~100 mg of calcite were first dissolved
275 using HNO_3 then spiked with a solution of a known $^{236}\text{U}/^{233}\text{U}/^{229}\text{Th}$ ratio.
276 Eichrom TRU-Spec resin columns were first decontaminated by using a
277 sequential wash of 1.5M HNO_3 , 4M HCl and 0.2M HF -0.1M HCl , then the U+Th
278 compound was separated from the carbonate matrix by using another wash of
279 1.5M HNO_3 , 4M HCl and 0.2M HF -0.1M HCl . The U+Th solution evaporated on a
280 hot plate at 80°C and later in 5% HNO_3 -0.5% HF , to be ready for the analyses in a
281 Nu Plasma multi-collector-inductively coupled plasma-mass spectrometer (MC-
282 ICP-MS), with settings defined in previous works⁴⁰. Final U-Th ages were
283 calculated using equation (1) of Hellstrom (2006)⁴¹ using the ^{230}Th - ^{234}U decay
284 constants of Cheng et al. (2013)⁴² and an initial $(^{230}\text{Th}/^{232}\text{Th})_i$ of 1.5 ± 1.5 .
285 In Xi'an, the general chemical preparation procedure is similar to Melbourne,
286 although U and Th compounds, after calcite HNO_3 dissolution, are first
287 precipitated using a Fe solution, then extracted separately by using
288 decontaminated resin columns and sequential washes of 6N HCl and ultraclean
289 water. The U and Th solution is mixed with 2% HNO_3 + 0.1% HF before analysis
290 on a Thermo Fisher Neptune Plus MC-ICP-MS⁴². Ages were calculated as above.
291 All ages are reported relative to 1950 AD (before present, BP; Supplementary
292 Table 1). Despite slight differences in sample chemical treatment and age
293 calculation, the dates produced in the two labs are consistent (Supplementary
294 Table 1). Only top and bottom were dated for the majority of speleothems
295 (Extended Data Figure 5), while 27 ages constitute the PC chronological dataset.
296 The PC ages and their 2σ uncertainties were used in StalAge⁴³ and COPRA⁴⁴ to
297 produce the age model. Both algorithms produced a comparable age-depth curve
298 (Extended Data Figure 6). In order to minimise the intrinsic artefacts produced
299 by the two algorithms, such as unrealistic maxima in growth rate and unjustified

300 large uncertainty propagation, the final age model was obtained by a linear
301 regression of the average age values between StalAge and COPRA models at the
302 same depths (Extended Data Figure 6).

303 For stable isotopes, powders were prepared using an online, continuous-flow
304 preparation system (GasBench II), then analysed using a ThermoFisher Delta V
305 Plus mass spectrometer at the University of Innsbruck (Austria), Institute of
306 Geology. NBS18, NBS19, CO1, and CO8 standards were used as references. The
307 results are expressed in per mil (‰) units relative to the Vienna Pee Dee
308 Belemnite (VPDB) international standard. The 1σ analytical reproducibility was
309 0.06‰ and 0.08‰ for $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$, respectively.

310

311 **Conditions during PC deposition**

312 Stable isotope values of speleothems deposited under non-equilibrium
313 conditions may mask the palaeoclimate signal. The Hendy test can be used to
314 evaluate geochemical conditions during calcite deposition⁴⁵, and equilibrium is
315 indicated if: 1) $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values are not strongly correlated along the growth
316 axis; 2) $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values are not strongly positively correlated from the
317 centre to the flank along individual growth layers; 3) $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ do not
318 increase from the centre to the side of growth layer, with a maximum increase
319 threshold of 0.8‰ for $\delta^{18}\text{O}$. $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values along the central axis of PC are
320 not strongly correlated ($r = 0.6$ – although correlation itself might be a result of
321 climate forcing⁴⁶), and individual layers do not suggest non-equilibrium
322 fractionation (Extended Data Figure 7). A slight influence of kinetic fractionation
323 is only likely for the H1 layer (Extended Data Figure 7), located close to the top of
324 the speleothem and starting at 10 mm from the centre of the stalagmite. In this
325 top part, the stalagmite diameter is small, and the more positive $\delta^{18}\text{O}$ values
326 resulted from the steep flank.

327 In addition to the Hendy test, the constant ~ 10 cm diameter of PC also argues in
328 favour of equilibrium-dominated isotope fractionation⁴⁷.

329 Finally, we consider Pozzo Cucù cave a ventilation-poor environment during PC
330 deposition, considering the present narrow artificial entrance. Indeed, Pozzo
331 Cucù possibly belongs to a karst system that had no large natural connection
332 with the surface, minimizing the air exchange between the cave and the surface.
333 This is important because ventilation is the main driver of fast degassing and
334 evaporation in caves (considering that humidity in non-ventilated caves is
335 commonly close to condensation), with evaporation being one of the principal
336 causes of kinetic fractionation. However, it is suspected that speleothems are
337 never deposited at full equilibrium conditions⁴⁶, and we cannot exclude a small
338 influence of kinetic fractionation in the PC stable isotope signature. For this
339 reason, and based on our previous studies^{27,48,49}, PC is considered as deposited
340 under quasi-equilibrium conditions, i.e. $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ data primarily reflect
341 palaeoclimate/palaeoenvironmental conditions above the cave.

342 Regarding post-depositional processes that might have compromised the
343 original geochemical composition of the stalagmite, PC does not show any visual
344 evidence of dissolution and recrystallization. Accordingly, all U-Th dates are in
345 stratigraphic order (Supplementary Table 1).

346

347 **Significance of $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ values**

348 Speleothem $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ ($\delta^{13}\text{C}_{\text{spel}}$ and $\delta^{18}\text{O}_{\text{spel}}$) values reflect processes *inside*
349 and *outside* of the karst system. Because endogenous (i.e. geological) processes
350 might conceal and/or modify the geochemical output of exogenous (i.e. climatic)
351 processes, the first challenge in speleothem science is to understand whether or
352 not a potential climate signal has been registered in the stalagmite stable isotope
353 signature. With calcite deposited under quasi-equilibrium conditions and with
354 no evidence of diagenesis, endogenous factors can be ruled out as primary
355 drivers of stable isotopic composition. Furthermore, considering that most of
356 PC's $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ ($\delta^{13}\text{C}_{\text{PC}}$ and $\delta^{18}\text{O}_{\text{PC}}$) shifts occurred simultaneously with
357 interhemispheric climate events (Fig. 2 and 3), it is clear that climate had a major
358 role in modulating stable isotopes. The interpretation of $\delta^{13}\text{C}_{\text{PC}}$ and $\delta^{18}\text{O}_{\text{PC}}$
359 timeseries hence requires to identify the key exogenous factor(s) and to
360 understand if endogenous factors had a secondary role in modulating $\delta^{13}\text{C}_{\text{PC}}$ and
361 $\delta^{18}\text{O}_{\text{PC}}$ values.

362 At Western Europe latitudes, temperature and rainfall amount compete in
363 regulating rainfall water $\delta^{18}\text{O}$ ($\delta^{18}\text{O}_{\text{rw}}$). Temperature and $\delta^{18}\text{O}_{\text{rw}}$, in the
364 Mediterranean region, show a weak positive gradient of $\sim 0.22\text{‰}/\text{°C}$, while
365 rainfall amount and $\delta^{18}\text{O}_{\text{rw}}$ show a strong negative gradient of $\sim -1.6\text{‰}/100\text{ mm}$
366 rain⁵⁰. The equilibrium $\delta^{18}\text{O}$ fractionation during calcite deposition ranges
367 between $-0.24\text{‰}/\text{°C}$ (⁵¹) and $-0.18\text{‰}/\text{°C}$ (⁵²) and counterbalances the
368 temperature-dependent isotope fractionation of atmospheric precipitation
369 outside the cave. Accordingly, rainfall amount is the principal driver of $\delta^{18}\text{O}_{\text{spel}}$ in
370 the study area as supported by previous studies in the western
371 Mediterranean^{18,23,27,48,49,53}. The same effect prevails in Central Italy⁵⁴, the
372 nearest speleothem record from Italy, as well as in Macedonia (F.Y.R.O.M)⁵⁵, the
373 nearest speleothem record on the Balkan side of the Adriatic Sea. However,
374 rainfall amount oscillations should also affect the rate of bedrock dissolution that
375 in turn could have an important impact on growth rate and the abundance of
376 uranium in speleothems. During wet (and warm) climate stages, bedrock is
377 subjected to a more intense dissolution because of the higher quantity of water
378 and a higher input of CO_2 from soil. Because of the higher amount of dissolved
379 carbonate in the drip water and a possibly faster dripping in the cave,
380 speleothem growth rate increases. The opposite (i.e. a growth rate decrease) is
381 expected for dry stages, although this general condition might not be valid for
382 complex karst networks and/or might vary with time⁵⁶. At the same time, rapid
383 dissolution of bedrock limits uranium alpha-recoil, i.e. ^{234}U and ^{238}U are equally
384 leached from the bedrock²³. Longer water residence times, typical of drier
385 conditions, promote uranium alpha-recoil and higher $[\text{}^{234}/\text{}^{238}\text{U}]_i$ ratios because of
386 a more efficient leaching of ^{234}U . If rainfall amount is the main regulator of
387 $\delta^{18}\text{O}_{\text{PC}}$, more negative values are expected during relatively wet periods, when
388 growth rate increases and $[\text{}^{234}/\text{}^{238}\text{U}]_i$ ratio decreases; on the contrary, less
389 negative values are expected during relatively dry periods when growth rate
390 decreases and the $[\text{}^{234}/\text{}^{238}\text{U}]_i$ ratio increases. PC shows, within uncertainties, this
391 pattern, confirming that rainfall amount was one of the principal driver of $\delta^{18}\text{O}_{\text{PC}}$
392 (Extended Data Figure 4). The agreement between the $\delta^{18}\text{O}_{\text{PC}}$ pattern and the
393 Greenland isotope record for most of the DO cycles, with more negative values
394 during interstadials and less negative values during stadials, is an indirect
395 confirmation of the rainfall amount effect as interstadials (stadials) were
396 relatively wet (dry) in the Mediterranean realm^{18,27,48,49,54}.

397 Vegetation bioproductivity controls $\delta^{13}\text{C}$ of soil CO_2 ($\delta^{13}\text{C}_{\text{soil}}$) and thus $\delta^{13}\text{C}$ in the
398 infiltrating water ($\delta^{13}\text{C}_{\text{iw}}$). Excluding endogenous factors, $\delta^{13}\text{C}_{\text{spel}}$ ranges between
399 -14.0‰ and -5.0‰ for C3 plants²². More negative $\delta^{13}\text{C}_{\text{iw-spel}}$ values are expected
400 during periods of high bioproductivity, characteristic of humid and warm climate
401 stages, while less negative $\delta^{13}\text{C}_{\text{iw-spel}}$ values are expected during periods of low
402 bioproductivity, typical of dry and cold climate stages. $\delta^{13}\text{C}_{\text{PC}}$ shows the most
403 significant oscillation during MIS 5 and 4, with lower values corresponding to
404 interstadials and higher values corresponding to stadials, in agreement with
405 $\delta^{18}\text{O}_{\text{PC}}$ oscillations. The only exogenous process that could cause a substantial
406 increase in $\delta^{13}\text{C}_{\text{iw-spel}}$ is the switch to C4 vegetation²². At the same time,
407 endogenous phenomena such as sulphide-driven bedrock dissolution⁵⁷, closed-
408 system bedrock dissolution⁴⁵ and prior calcite precipitation (PCP)⁵⁸ also push
409 $\delta^{13}\text{C}_{\text{iw-spel}}$ toward less negative values. Importantly, all these processes can be
410 attributed to a relative dry climate, considering that C4 plants thrive in steppe-
411 like environments and the endogenous processes are enhanced during times of
412 reduced recharge. However, only PCP has an effect on both $\delta^{13}\text{C}_{\text{iw-spel}}$ and $\delta^{18}\text{O}_{\text{iw-}}$
413 spel .

414 Concomitant variations of $\delta^{13}\text{C}_{\text{PC}}$ and $\delta^{18}\text{O}_{\text{PC}}$ during MIS 5 to 4 are thus attributed
415 to rainfall and bioproductivity changes triggered by the interstadial-stadial
416 cyclicity. However, during the concomitant excursion toward the highest values
417 at $105.2^{+2.4}/_{-2.3}$ to $102.4^{+2.1}/_{-2.0}$ ka, $95.7^{+0.9}/_{-0.8}$ to $93.1^{+0.7}/_{-0.9}$ ka, $66.7^{+0.9}/_{-1.2}$ to
418 $65.6^{+1.1}/_{-1.3}$ ka, and $55.3^{+1.1}/_{-2.5}$ to $54.9^{+1.1}/_{-2.7}$ ka and especially when $\delta^{13}\text{C}_{\text{PC}}$ is
419 above $\sim -5\text{‰}$ it is possible that the above-mentioned processes might have
420 played a role in increasing $\delta^{13}\text{C}_{\text{PC}}$ and $\delta^{18}\text{O}_{\text{PC}}$. We consider PCP as the main
421 endogenous process increasing $\delta^{13}\text{C}_{\text{iw}}$ and $\delta^{18}\text{O}_{\text{iw}}$, because rapid shifts in $\delta^{13}\text{C}_{\text{PC}}$
422 and $\delta^{18}\text{O}_{\text{PC}}$ toward high values occur simultaneously. Sulphide-driven bedrock
423 dissolution can be excluded because of the lack of sulphide minerals in the Pozzo
424 Cucù bedrock.

425 During MIS 3, $\delta^{13}\text{C}_{\text{PC}}$ and $\delta^{18}\text{O}_{\text{PC}}$ do not covary. $\delta^{13}\text{C}_{\text{PC}}$ shows a pattern
426 characterised by negligible oscillations with values around $\sim -8\text{‰}$; $\delta^{18}\text{O}_{\text{PC}}$ shows
427 millennial-scale DO-like oscillations of $\sim -1\text{‰}$, lower than during MIS 5 and 4,
428 and a general trend toward less negative values. The lack of a covariation
429 between $\delta^{13}\text{C}_{\text{PC}}$ and $\delta^{18}\text{O}_{\text{PC}}$ argues against PCP; mixing of groundwater or in-karst
430 kinetic processes (for example: evaporation) are excluded for the same reason.
431 The relatively negative values of $\sim -8\text{‰}$ are inconsistent with closed system and
432 sulphide-driven bedrock dissolution. Even speleothems deposited from water in
433 contact with CO_2 derived from old organic matter trapped in bedrock fissures
434 would result in $\delta^{13}\text{C}$ values higher than $\sim -8\text{‰}$. Thus, $\delta^{13}\text{C}_{\text{PC}}$ reflects soil
435 bioproductivity, which remained rather stable throughout MIS 3. This means
436 that variations in rainfall (and temperature) during MIS 3 in Apulia were too
437 small to cause significant perturbations in $\delta^{13}\text{C}_{\text{soil}}$. This limited rainfall variation,
438 together with a decreased resolution in this part of the record could explain the
439 small $\sim -1\text{‰}$ excursions of $\delta^{18}\text{O}_{\text{PC}}$.

440 Finally, $\delta^{18}\text{O}_{\text{PC}}$ possibly responded to variations of moisture source during the
441 entire MIS 5 to 3 period. Today, the study area receives most rainfall from the
442 Atlantic, with a smaller contribution from the Mediterranean Sea⁵⁹. Atlantic-
443 sourced $\delta^{18}\text{O}_{\text{rw}}$ is more negative than Mediterranean-sourced $\delta^{18}\text{O}_{\text{rw}}$, and the
444 influence of the former is related to: 1) abundance of moisture produced in the
445 Atlantic and 2) the efficiency of the Westerlies delivering this moisture in the

446 Mediterranean area. When polar ice sheets expanded, the influence of Atlantic-
447 sourced moisture decreased in favour of Mediterranean-sourced moisture,
448 because the production of moisture in the Atlantic is lower and westerlies
449 trajectories changes. With all the other effects negligible, the source effect⁶⁰
450 would generally follow DO cyclicity leading to more negative $\delta^{18}\text{O}$ values during
451 interstadials and less negative values during stadials. However, at some point in
452 the MIS 3, the Westerlies were pushed southward in response to the expansion
453 of the Northern ice sheet. Rainfall in the Mediterranean was then controlled by
454 the genesis of low pressure areas (cyclones) within in the Mediterranean realm.
455 Although periods of increasing versus decreasing rainfall might still follow
456 regional-scale DO cyclicity, rainfall amount changes are inferior than during MIS
457 5 and 4, because the availability of moisture is lower than when the Atlantic is
458 the principal moisture source. A possible interpretation of the $\delta^{18}\text{O}_{\text{PC}}$ signature
459 during MIS 3 invokes a major influence of Mediterranean-derived rainfall
460 causing a gradual trend of rainfall reduction, with a superimposed low-intensity
461 rainfall amount increase versus decrease pattern (following DO cyclicity). It is
462 important to stress that both the gradual rainfall reduction as well as rainfall
463 decrease during MIS 3 GIs in Apulia were insufficient to cause significant
464 perturbations in $\delta^{13}\text{C}_{\text{soil}}$, as for example during MIS 5 and 4.
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492 **Competing interests**

493
494 The authors declare no competing interests

495 **Data availability**
496 Supplementary Table 1 and 2
497

498 **Authors contribution**

499 AC and VC conceived and designed the experiments, AC, VC, CS, JH, HC performed
500 the experiments, AC and SB analyzed the data, AC, VC, CS, SB, JDW contributed
501 with materials/analysis tools, AC wrote the paper with inputs from all coauthors.
502

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739 **Figure 1.** A) PC stalagmite, sampling information and age model (see methods
740 for age model construction and Hendy test). B) Ages of published Italian
741 stalagmites used for palaeoclimate reconstruction and those presented in this
742 study, compared to interglacial versus glacial variation over the last ~500 ka
743 (curves: Greenland ice core $\delta^{18}\text{O}$ (purple)¹⁵ and Atlantic benthic foraminifera
744 $\delta^{18}\text{O}$ (black)⁶¹. The background shows a map of Italy with the location of the
745 studied cave (red star) and other published speleothem records. Ages are
746 marked by dots; solid lines indicate continuous growth while dotted lines stand
747 for discontinuous growth and/or poor chronological constraint. Only
748 speleothems from Apulia (this study, red labels) continuously grew over the
749 entire last glacial period (gray shade). Speleothems: PE (Piani Eterni karst
750 system)⁴⁸, ER (Ernesto Cave)⁶², CB (Cesare Battisti Cave)⁶³, Sa (Savi Cave)⁶⁴, Ba
751 (Basura Cave)⁶⁵, RM (Rio Martino Cave)⁶⁶, TCU (Tana che Urla Cave)⁶⁷, GDV
752 (Grotta del Vento)⁶⁸, Ren (Renella Cave)⁶⁹, CC (Corchia Cave)⁵³, Gypsum
753 (Northern Italy Gypsum caves)⁶⁹, Fr (Frasassi Cave)^{16,54}, SA (Sant'Angelo Cave,
754 this study), Za (Zaccaria Cave, this study), Tr (Trullo Cave, this study), PC (Pozzo
755 Cucù Cave, this study), BMS (Bue Marino Cave)⁴⁹, CA (Crovasa Azzurra Cave)²⁷,
756 Car (Carburangeli Cave)⁷⁰.

757
758 **Figure 2.** PC $\delta^{13}\text{C}$ (top, red) and $\delta^{18}\text{O}$ (bottom, blue) versus Greenland ice core
759 $\delta^{18}\text{O}$ (middle, black)¹⁵. Black numbers and bars refer to DO cycles²⁵. The PC
760 proxy record is correlated to NGRIP along stadial events (grey shading).
761 Intermittent shading is used when correlation is ambiguous. Boxes on the
762 bottom show MIS and H events, as well as the Neanderthal-MH transition in
763 Apulia and MUPT in Europe. PC $\delta^{13}\text{C}$ and $\delta^{18}\text{O}$ curves also show age 2σ -
764 uncertainties (shaded horizontal bars).

765
766 **Figure 3.** PC $\delta^{18}\text{O}$ record (grey) compared to marine (a. GDEC-4-2³⁰) and
767 lacustrine (b. Monticchio Lake²⁸; c. Tenaghi Philippon Lake²⁹; d. Ohrid Lake⁷¹)
768 archives, as well as circum-Mediterranean speleothems (e. Cueva Victoria $\delta^{18}\text{O}$,
769 yellow line¹⁷ (refer to black axis/numbers); Ejulve Cave $\delta^{13}\text{C}$, purple line¹¹;
770 Buraca Gloriosa, pink line¹⁸; Sofular Cave $\delta^{18}\text{O}$, green line¹⁹ (refer to black
771 axis/numbers); Corchia Cave $\delta^{18}\text{O}$, orange dotted line⁵³; Frasassi Cave
772 (composite), orange line¹⁶ g. Villars Cave $\delta^{18}\text{O}$, green line¹⁰; NALPS19 record
773 $\delta^{18}\text{O}$, blue line⁷²; h. Soreq cave $\delta^{18}\text{O}$, brown line¹⁹).

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