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

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

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

Background

There is no leading theory about the triggers of the most important cultural transition in human history[1,2]. Rapid climate shifts during the MUPT are considered as one of the most important drivers of the Neanderthal-MH interchange[2-8], because of the impact on population/depopulation dynamics[7,8], fragmentation of optimal habitats[6], deterioration of environmental conditions[3], and/or the weakening of local communities after severe cold and dry stages[4]. Accordingly, the Neanderthals have been inexorably afflicted by recurrent millennial- to centennial-scale dry and cold conditions attributable to Dansgaard–Oeschger (DO) cycles and especially Heinrich (H) events during Marine Isotope Stage (MIS) 3. H events induced aridity and cold temperatures in Western and Central Europe[10], and those occurring from ~63 to ~40.5 ka (H6 to H4) had irreversible impacts on the Neanderthal population[5]. The one at ~40.5 ka (H4) caused the final Neanderthals' demise and/or their migration into other areas where the extinction occurred later[2]. However, this is at odds with the fact that H events lack consistent equivalents in the Mediterranean realm[11] and they may have not necessarily resulted in very harsh climate conditions in the entire region[12]. Additionally, Neanderthal extinction might have occurred before H4[13]. Indeed, there are chronological and spatial impediments in solving this conundrum, because of age uncertainties of both the palaeoclimate and the anthropological events, and the unknown response of local Neanderthal-MH habitats to high-latitude driven climate change. Moreover, ancient human communities occupied only small portions of land with ideal settlement conditions, and the gradual climate deterioration of the last glacial period likely reduced the extent of these optimal Neanderthal habitats[6]. The 2,600 to 5,400 years-long interval of Neanderthal-MH coexistence was likely unevenly

distributed in space[13]. Therefore, climate-related hypotheses should be based on records from the same area where Neanderthals-MH actually cohabitated, but these records are scarce[14].
Neanderthal and MH remains are widespread from northern to southern Italy[9]. This study targets Apulia (Fig. 1), where Neanderthals were present since at least MIS 5e until ~42 ka, while the earliest European MH appeared in this region ~45 ka[1,9]. Thus, this is a strategic region for understanding the biocultural processes occurring during the Neanderthal-MH transition and, ultimately, whether climate played a decisive role in the disappearance of the former and in the territorial supremacy of the latter.

Results

We explored several caves in Apulia searching for speleothems (Extended Data Figure 1). Uranium-thorium (U-Th) radiometric dating on 14 stalagmites (Extended Data Figure 5 and Supplementary Table 1) attests that cave calcite deposition was abundant during the last and older glacial periods (Fig. 1). Here we focus on stalagmite PC from Pozzo Cucù Cave (40.90° N, 17.16° E), for which 27 stratigraphically aligned U-Th dates (Supplementary Table 1) were used to produce an age-depth model (Extended Data Figure 6). Accordingly, PC grew uninterruptedly from 106.0 $^{+2.8}/_{-2.7}$ to 26.6 $^{+0.8}/_{-0.9}$ ka, and thus covers MIS 5 to MIS 3 (Fig. 2). High-resolution $\delta^{18}O$-$\delta^{13}C$ analyses (n = 2659) reveal a pattern comparable to the North Greenland Ice Core[15] (NGRIP) from the entire MIS 5 and 4. During MIS 3, $\delta^{18}O$ shows a less evident – but still recognisable – similarity with NGRIP, while $\delta^{13}C$ yields a plateau-like signal. Importantly, $\delta^{18}O$-$\delta^{13}C$ does not show evidence of many of the most severe climate events affecting northern latitudes (e.g., Heinrich events).

Discussion

Because glacial stages in the Mediterranean area were generally dry and characterised by sparse vegetation, continuous speleothem growth was rare. In Italy, for example, there is no evidence of uninterrupted stalagmite deposition during glacial periods (Fig. 1). To our knowledge, the longest record has been constructed by using four speleothems (two stalagmites and two stalactites) found in Frasassi Cave[16]. In the Iberian Peninsula, speleothem formation was also intermittent[11,17,18], while more continuous deposition is only known from caves in Turkey and on the south-eastern side of the Mediterranean Sea[19,20]. The continuous growth of speleothems in Manot Cave (Israel) has been recently taken as evidence for the lack of water shortage in northern Israel during the last glacial period[21]. Considering that continuous speleothem deposition is only feasible if the karst reservoir is recharged by rainfall and soil bioactivity procures high amounts of CO_2 to infiltrating water, Apulia's glacial climate was possibly milder than in other areas in the western and central Mediterranean.

The $\delta^{13}C$ values of PC are representative of soil activity[10,11] (see methods). For most of the time, values are more negative than -5.0 ‰ (Fig. 2), attesting the presence of C3 plants[22] that normally prevail in temperate regions.

It is well established that $\delta^{18}O$ in speleothems from the Mediterranean principally reflects rainfall amount variations[23]. Secondarily, it might also record changes in moisture sources[24]. Because of the striking resemblance between PC-$\delta^{18}O$ and NGRIP $\delta^{18}O$ (Fig. 2), especially during MIS 5 and 4, we are confident that the stalagmite recorded the effects of climate change in the high latitudes and the North Atlantic. This intrahemispheric connection is translated into rainfall oscillations during DO cycles, with higher (lower) rainfall amount during interstadials (stadials) as expressed by more negative (positive) $\delta^{18}O$ values. This correlation can also be seen at the intra-stadial/interstadial timescale[25] (Extended Data Figure 2). Intriguingly, the shape of several MIS 5 DO-like events in PC (e.g., DOs from ~90 to ~70 ka) appear more similar to the Asian monsoonal oscillations[26] than to NGRIP (Extended Data Figure 3), a feature worth to be examined in detail in future studies. Variability of PC growth rate and $[^{234/238}U]_i$ (Extended Data Figure 4) agrees with PC-$\delta^{18}O$ being principally driven by rainfall amount (see methods). Changes in the dominant moisture source are possibly reflected by the PC-$\delta^{18}O$ values too. During Greenland Interstadials (GIs) rainfall in the Mediterranean region was predominantly Atlantic-sourced giving rise to more negative $\delta^{18}O$ values, similar to today[23,27]. Conversely, Mediterranean-sourced moisture showing more positive $\delta^{18}O$ values prevailed when large ice sheets during Greenland Stadials (GSs) impeded the Westerlies from efficiently delivering moisture to the Mediterranean region (see methods). This is because the lower moisture production in the Atlantic, according to the relative decrease of GSs temperatures, limits advection over the Mediterranean[23]. As the Atlantic moisture input decreases, the ratio between Mediterranean/Atlantic moisture increases in the area of study. The further expansion of northern ice-sheet since MIS 3 probably caused a pronounced southward shift of the Westerlies[24], that might have boosted this mechanism.

The covariation of $\delta^{18}O$ and $\delta^{13}C$ in PC is consistent with rainfall amount being a primary driver (Fig. 2). In Apulia, rainfall coupled with temperature variations as recorded by other archives (Fig. 3) modulated soil organic activity reflected by the $\delta^{13}C$ record of PC (Fig. 2). Between DO 24 and DO 15, bioproductivity increased during GIs giving rise to more negative $\delta^{13}C$ values. Because of reduced rainfall and lower temperatures during GSs, bioproductivity decreased resulting in more positive $\delta^{13}C$ values. The generally low $\delta^{13}C$ values in conjunction with the lack of growth stops in PC strongly argues for a continuously vegetated catchment of the cave's drip water with expanding forests during GIs and trees becoming sparse during GSs (Fig. 3), in agreement with nearby pollen records[28,29]. The PC $\delta^{18}O$-$\delta^{13}C$ data suggest two periods of extremely dry condition, when both isotopes show peak values: from $66.7\ ^{+0.9}/_{-1.2}$ to $65.6\ ^{+1.1}/_{-1.3}$ ka during MIS 4, and from $55.3\ ^{+1.1}/_{-2.5}$ to $54.9\ ^{+1.1}/_{-2.7}$ ka during MIS 3. Both events deviate from the NGRIP variability but agree with speleothem[11], lacustrine[29] and marine records[30] from the Mediterranean region. They have been attributed to markedly dry conditions during ice-rafting events and increases of cold-water foraminifera in the North Atlantic during H events 6 and 5a[11,31]. Although the aridity of these events was not sufficient to stop carbonate deposition at the PC site, as occurring in speleothems from continental Europe[10] (Fig. 3g), these periods are here regarded as the driest and probably coldest of the entire MIS 5 to 3 timespan at least in Southern Italy. The event at ~55 ka was certainly the driest of the entire record as reflected by the highest $\delta^{13}C$ values and a marked reduction in growth rate (Fig. 1 and Extended Data 4). This event was likely even drier than GS24 and GS23, from $105.2\ ^{+2.4}/_{-2.3}$ to $102.4^{+2.1}/_{-2.0}$ ka and from $95.7\ ^{+0.9}/_{-0.8}$ to $93.1\ ^{+0.7}/_{-0.9}$ ka, which also led to $\delta^{13}C$ values higher than -5 ‰.

There is no correlation between PC-$\delta^{18}O$ and NGRIP for DO 14 and 13 (Fig. 2), likely because of the low resolution due to the slow growth rate. From DO 12 to the top of the record, PC shows its most interesting features: i) PC-$\delta^{18}O$ reveals NGRIP-like millennial-scale oscillations, although the similarities with NGRIP are strikingly less evident than prior to ~55 ka. The implication is that rapid climate oscillation during MIS 3 recorded in Greenland had a lower impact on rainfall variability in Apulia than those during MIS 5 and 4; and ii) these oscillations are superimposed to a general PC-$\delta^{18}O$ trend toward more positive values (Fig. 2), which is synchronous with the progressive reduction of the stalagmite's diameter (Fig. 1). Considering that the latter mirrors long-lasting reduced dripping and thus calcite deposition at the top of the speleothem[32], these observations point to a middle to upper MIS 3 in Apulia characterised by a progressive rainfall reduction rather than by rapid and severe climate switches. At this point the Mediterranean might have become the primary source of moisture because of the expansion of the Northern ice-sheets. This is consistent with a gradual increase in the $\delta^{18}O$ value of the moisture source for PC. Furthermore, rainfall amount variability during MIS 3 GIs and GSs, caused by Mediterranean cyclogenesis, is not comparable to that induced by a higher efficiency of Westerlies delivering moisture during MIS 4 and 5. This is because the availability of moisture is lower than when the Atlantic is the principal moisture source. Most importantly, from ~55 ka onward PC $\delta^{13}C$ values show a "plateau-like" feature during MIS 3 (Fig. 2). This cannot be explained by in-karst processes and/or kinetic mechanisms affecting isotopic fractionation (see methods), but rather reflects stable soil dynamics and only minor vegetation changes. Preliminary $\delta^{18}O$-$\delta^{13}C$ data from another Apulian stalagmite (SA1, Fig. 2 and Extended Data 5) agree with PC[33]. This reinforces the idea that drastic rainfall (and temperature) variations were minimal and insufficient to cause major changes in soil bioproductivity and/or interruptions in speleothem deposition. Speleothems from Frasassi cave[16], the only Italian record available for comparison (Fig. 1), also report ~constant $\delta^{18}O$-$\delta^{13}C$ (Fig. 3) from ~55 ka to at least ~30 ka, which was interpreted as mirroring relatively stable climatic conditions in the northeastern Apennines. The slight depletion trend that is visible in the PC-$\delta^{13}C$ plateau may appear inconsistent with the gradual decrease in rainfall expressed by PC-$\delta^{18}O$. We advance the possibility that the lack of severe droughts, which would also cause the total/partial soil erosion, allowed an enduring maturation of pedogenic layers although the general trend of climate deterioration. This hypothesis will be thoroughly explored by future studies. Vegetation shifts likely occurred, but they were possibly less pronounced than in the nearby Monticchio Lake[28] area (Fig. 3) because of the proximity with the coast and the lower altitude.

Accordingly, from ~55 ka onward we set the beginning of environmental niche conditions in Apulia[1]. Neanderthals settled in this region well before MIS 3, so Apulia cannot be considered a *refugia*[34] for them. Contrarily to Apulia, freshwater availability, as well as vegetation, was scarce in the northern parts of the Italian Peninsula as highlighted by speleothem deposition (Fig. 1). This attracted wildlife and new hunter-gatherer communities.

Favourable settlement conditions might have fostered the arrival of MH in Apulia and their coexistence with Neanderthals (Fig. 2). The disappearance of Neanderthals in Apulia (~42 ka) occurred ~13,000 years after the cold and dry interval at ~55 ka, while the following H5 (~45 ka) apparently did not have a strong impact on the local environment. This is confirmed by arboreal pollen values above 40% in the nearby Monticchio Lake record[28]. In contrast, pollen in Greece[29], planktonic foraminifera in the Tyrrhenian Sea[30] and speleothems from Iberia[11] and Turkey[19] record climate deterioration during H5 at around 48 ka (Fig. 3), further suggesting that Apulia was a favourable environmental niche during MIS 3 in comparison to other localities. It has been recently shown[35] that the climate in Morocco responded inconsistently to northern high-latitude ice-rafted debris events, with even pluvial phases occurring during these cold and dry periods. This calls for a re-evaluation of the role of the northern high latitudes in triggering major cooling/drying events across the Mediterranean region. Even supposing a late Neanderthal presence in Southern Italy, e.g. later than ~42 ka, the fact that the impact of H4 (~40.5 ka) on PC's proxy data is negligible further excludes climate as the major trigger for the Neanderthal-MH turnover during MUPT.

Final remarks

PC represents strong evidence of environmental stability in Apulia during the Neanderthal-MH turnover, hence high latitude rapid climate changes were not the primary cause of Neanderthals' disappearance in this region. Opposite opinions face the paradox that shifts toward a dry and cold climate did not result in a cessation of speleothem deposition, but caused the extinction of a species well adapted to the surrounding environment and that survived previous climate periods more severe than MIS 3. Consequently, this applies to all European mid-latitude regions where DO climate variations during MIS 3 were attenuated by latitudinal, orographic and/or geographical factors. In all Apulia-like niches, the issue of the Neanderthal-MH turnover must be approached from a perspective that takes into account climate and environmental conditions favourable for both species. This interestingly differs from the Levantine area where there was no water shortage during MUPT, but speleothem $\delta^{13}C$ suggest an alternation between woody and more open vegetation. The adaptation of different modern cultures that possibly interacted with Neanderthals has been there defined as landscape-dependent[21]. In Apulia-like niches instead, the advanced hunting technology of MH groups over Neanderthals since their migration to Europe[36-39] appears now a solid reason to explain the territorial supremacy of the former that induced the extinction of the latter after ~3000 years of coexistence.

Methods

Cave sampling and speleothem subsampling

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

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

The majority of U-Th dating was accomplished at the University of Melbourne (Australia), School of Earth Sciences, while a minor part was carried out at the Xi'an Jiaotong University (China), Institute of Global Environmental Change (Supplementary Table 1). In Melbourne, ~100 mg of calcite were first dissolved using HNO_3 then spiked with a solution of a known $^{236}U/^{233}U/^{229}Th$ ratio. Eichrom TRU-Spec resin columns were first decontaminated by using a sequential wash of 1.5M HNO_3, 4M HCl and 0.2M HF-0.1M HCl, then the U+Th compound was separated from the carbonate matrix by using another wash of 1.5M HNO_3, 4M HCl and 0.2M HF-0.1M HCl. The U+Th solution evaporated on a hot plate at 80˚C and later in 5% HNO_3-0.5% HF, to be ready for the analyses in a Nu Plasma multi-collector–inductively coupled plasma–mass spectrometer (MC-ICP-MS), with settings defined in previous works[40]. Final U–Th ages were calculated using equation (1) of Hellstrom (2006)[41] using the ^{230}Th–^{234}U decay constants of Cheng et al. (2013)[42] and an initial $(^{230}Th/^{232}Th)_i$ of 1.5±1.5.

In Xi'an, the general chemical preparation procedure is similar to Melbourne, although U and Th compounds, after calcite HNO_3 dissolution, are first precipitated using a Fe solution, then extracted separately by using decontaminated resin columns and sequential washes of 6N HCl and ultraclean water. The U and Th solution is mixed with 2% HNO_3 + 0.1% HF before analysis on a Thermo Fisher Neptune Plus MC-ICP-MS[42]. Ages were calculated as above. All ages are reported relative to 1950 AD (before present, BP; Supplementary Table 1). Despite slight differences in sample chemical treatment and age calculation, the dates produced in the two labs are consistent (Supplementary Table 1). Only top and bottom were dated for the majority of speleothems (Extended Data Figure 5), while 27 ages constitute the PC chronological dataset. The PC ages and their 2σ uncertainties were used in StalAge[43] and COPRA[44] to produce the age model. Both algorithms produced a comparable age-depth curve (Extended Data Figure 6). In order to minimise the intrinsic artefacts produced by the two algorithms, such as unrealistic maxima in growth rate and unjustified large uncertainty propagation, the final age model was obtained by a linear regression of the average age values between StalAge and COPRA models at the same depths (Extended Data Figure 6).

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

Conditions during PC deposition

Stable isotope values of speleothems deposited under non-equilibrium conditions may mask the palaeoclimate signal. The Hendy test can be used to evaluate geochemical conditions during calcite deposition[45], and equilibrium is indicated if: 1) $\delta^{13}C$ and $\delta^{18}O$ values are not strongly correlated along the growth axis; 2) $\delta^{13}C$ and $\delta^{18}O$ values are not strongly positively correlated from the centre to the flank along individual growth layers; 3) $\delta^{13}C$ and $\delta^{18}O$ do not increase from the centre to the side of growth layer, with a maximum increase threshold of 0.8‰ for $\delta^{18}O$. $\delta^{13}C$ and $\delta^{18}O$ values along the central axis of PC are not strongly correlated ($r = 0.6$ – although correlation itself might be a result of climate forcing[46]), and individual layers do not suggest non-equilibrium fractionation (Extended Data Figure 7). A slight influence of kinetic fractionation is only likely for the H1 layer (Extended Data Figure 7), located close to the top of the speleothem and starting at 10 mm from the centre of the stalagmite. In this top part, the stalagmite diameter is small, and the more positive $\delta^{18}O$ values resulted from the steep flank.

In addition to the Hendy test, the constant ~10 cm diameter of PC also argues in favour of equilibrium-dominated isotope fractionation[47].

Finally, we consider Pozzo Cucù cave a ventilation-poor environment during PC deposition, considering the present narrow artificial entrance. Indeed, Pozzo Cucù possibly belongs to a karst system that had no large natural connection with the surface, minimizing the air exchange between the cave and the surface. This is important because ventilation is the main driver of fast degassing and evaporation in caves (considering that humidity in non-ventilated caves is commonly close to condensation), with evaporation being one of the principal causes of kinetic fractionation. However, it is suspected that speleothems are never deposited at full equilibrium conditions[46], and we cannot exclude a small influence of kinetic fractionation in the PC stable isotope signature. For this reason, and based on our previous studies[27,48,49], PC is considered as deposited under quasi-equilibrium conditions, i.e. $\delta^{13}C$ and $\delta^{18}O$ data primarily reflect palaeoclimate/palaeoenvironmental conditions above the cave.

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

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

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

At Western Europe latitudes, temperature and rainfall amount compete in regulating rainfall water $\delta^{18}O$ ($\delta^{18}O_{rw}$). Temperature and $\delta^{18}O_{rw}$, in the Mediterranean region, show a weak positive gradient of ~0.22‰/°C, while rainfall amount and $\delta^{18}O_{rw}$ show a strong negative gradient of ~-1.6‰/100 mm rain[50]. The equilibrium $\delta^{18}O$ fractionation during calcite deposition ranges between -0.24‰/°C ([51]) and -0.18‰/°C ([52]) and counterbalances the temperature-dependent isotope fractionation of atmospheric precipitation outside the cave. Accordingly, rainfall amount is the principal driver of $\delta^{18}O_{spel}$ in the study area as supported by previous studies in the western Mediterranean[18,23,27,48,49,53]. The same effect prevails in Central Italy[54], the nearest speleothem record from Italy, as well as in Macedonia (F.Y.R.O.M)[55], the nearest speleothem record on the Balkan side of the Adriatic Sea. However, rainfall amount oscillations should also affect the rate of bedrock dissolution that in turn could have an important impact on growth rate and the abundance of uranium in speleothems. During wet (and warm) climate stages, bedrock is subjected to a more intense dissolution because of the higher quantity of water and a higher input of CO_2 from soil. Because of the higher amount of dissolved carbonate in the drip water and a possibly faster dripping in the cave, speleothem growth rate increases. The opposite (i.e. a growth rate decrease) is expected for dry stages, although this general condition might not be valid for complex karst networks and/or might vary with time[56]. At the same time, rapid dissolution of bedrock limits uranium alpha-recoil, i.e. ^{234}U and ^{238}U are equally leached from the bedrock[23]. Longer water residence times, typical of drier conditions, promote uranium alpha-recoil and higher $[^{234/238}U]_i$ ratios because of a more efficient leaching of ^{234}U. If rainfall amount is the main regulator of $\delta^{18}O_{PC}$, more negative values are expected during relatively wet periods, when growth rate increases and $[^{234/238}U]_i$ ratio decreases; on the contrary, less negative values are expected during relatively dry periods when growth rate decreases and the $[^{234/238}U]_i$ ratio increases. PC shows, within uncertainties, this pattern, confirming that rainfall amount was one of the principal driver of $\delta^{18}O_{PC}$ (Extended Data Figure 4). The agreement between the $\delta^{18}O_{PC}$ pattern and the Greenland isotope record for most of the DO cycles, with more negative values during interstadials and less negative values during stadials, is an indirect confirmation of the rainfall amount effect as interstadials (stadials) were relatively wet (dry) in the Mediterranean realm[18,27,48,49,54].

Vegetation bioproductivity controls $\delta^{13}C$ of soil CO_2 ($\delta^{13}C_{soil}$) and thus $\delta^{13}C$ in the infiltrating water ($\delta^{13}C_{iw}$). Excluding endogenous factors, $\delta^{13}C_{spel}$ ranges between -14.0‰ and -5.0‰ for C3 plants[22]. More negative $\delta^{13}C_{iw-spel}$ values are expected during periods of high bioproductivity, characteristic of humid and warm climate stages, while less negative $\delta^{13}C_{iw-spel}$ values are expected during periods of low bioproductivity, typical of dry and cold climate stages. $\delta^{13}C_{PC}$ shows the most significant oscillation during MIS 5 and 4, with lower values corresponding to interstadials and higher values corresponding to stadials, in agreement with $\delta^{18}O_{PC}$ oscillations. The only exogenous process that could cause a substantial increase in $\delta^{13}C_{iw-spel}$ is the switch to C4 vegetation[22]. At the same time, endogenous phenomena such as sulphide-driven bedrock dissolution[57], closed-system bedrock dissolution[45] and prior calcite precipitation (PCP)[58] also push $\delta^{13}C_{iw-spel}$ toward less negative values. Importantly, all these processes can be attributed to a relative dry climate, considering that C4 plants thrive in steppe-like environments and the endogenous processes are enhanced during times of reduced recharge. However, only PCP has an effect on both $\delta^{13}C_{iw-spel}$ and $\delta^{18}O_{iw-spel}$.

Concomitant variations of $\delta^{13}C_{PC}$ and $\delta^{18}O_{PC}$ during MIS 5 to 4 are thus attributed to rainfall and bioproductivity changes triggered by the interstadial-stadial cyclicity. However, during the concomitant excursion toward the highest values 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 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 $\delta^{13}C_{PC}$ is above ~-5‰ it is possible that the above-mentioned processes might have played a role in increasing $\delta^{13}C_{PC}$ and $\delta^{18}O_{PC}$. We consider PCP as the main endogenous process increasing $\delta^{13}C_{iw}$ and $\delta^{18}O_{iw}$, because rapid shifts in $\delta^{13}C_{PC}$ and $\delta^{18}O_{PC}$ toward high values occur simultaneously. Sulphide-driven bedrock dissolution can be excluded because of the lack of sulphide minerals in the Pozzo Cucù bedrock.

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

Finally, $\delta^{18}O_{PC}$ possibly responded to variations of moisture source during the entire MIS 5 to 3 period. Today, the study area receives most rainfall from the Atlantic, with a smaller contribution from the Mediterranean Sea[59]. Atlantic-sourced $\delta^{18}O_{rw}$ is more negative than Mediterranean-sourced $\delta^{18}O_{rw}$, and the influence of the former is related to: 1) abundance of moisture produced in the Atlantic and 2) the efficiency of the Westerlies delivering this moisture in the

Mediterranean area. When polar ice sheets expanded, the influence of Atlantic-sourced moisture decreased in favour of Mediterranean-sourced moisture, because the production of moisture in the Atlantic is lower and westerlies trajectories changes. With all the other effects negligible, the source effect[60] would generally follow DO cyclicity leading to more negative $\delta^{18}O$ values during interstadials and less negative values during stadials. However, at some point in the MIS 3, the Westerlies were pushed southward in response to the expansion of the Northern ice sheet. Rainfall in the Mediterranean was then controlled by the genesis of low pressure areas (cyclones) within in the Mediterranean realm. Although periods of increasing versus decreasing rainfall might still follow regional-scale DO cyclicity, rainfall amount changes are inferior than during MIS 5 and 4, because the availability of moisture is lower than when the Atlantic is the principal moisture source. A possible interpretation of the $\delta^{18}O_{PC}$ signature during MIS 3 invokes a major influence of Mediterranean-derived rainfall causing a gradual trend of rainfall reduction, with a superimposed low-intensity rainfall amount increase versus decrease pattern (following DO cyclicity). It is important to stress that both the gradual rainfall reduction as well as rainfall decrease during MIS 3 GIs in Apulia were insufficient to cause significant perturbations in $\delta^{13}C_{soil}$, as for example during MIS 5 and 4.

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Competing interests

The authors declare no competing interests

Data availability

Supplementary Table 1 and 2

Authors contribution

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

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

Figure 2. PC $\delta^{13}C$ (top, red) and $\delta^{18}O$ (bottom, blue) versus Greenland ice core $\delta^{18}O$ (middle, black[15]). Black numbers and bars refer to DO cycles[25]. The PC proxy record is correlated to NGRIP along stadial events (grey shading). Intermittent shading is used when correlation is ambiguous. Boxes on the bottom show MIS and H events, as well as the Neanderthal-MH transition in Apulia and MUPT in Europe. PC $\delta^{13}C$ and $\delta^{18}O$ curves also show age 2σ-uncertainties (shaded horizontal bars).

Figure 3. PC $\delta^{18}O$ record (grey) compared to marine (a. GDEC-4-2[30]) and lacustrine (b. Monticchio Lake[28]; c. Tenaghi Philippon Lake[29]; d. Ohrid Lake[71]) archives, as well as circum-Mediterranean speleothems (e. Cueva Victoria $\delta^{18}O$, yellow line[17] (refer to black axis/numbers); Ejulve Cave $\delta^{13}C$, purple line[11]; Buraca Gloriosa, pink line[18]; f. Sofular Cave $\delta^{18}O$, green line[19] (refer to black axis/numbers); Corchia Cave $\delta^{18}O$, orange dotted line[53]; Frasassi Cave (composite), orange line [16] g. Villars Cave $\delta^{18}O$, green line[10]; NALPS19 record $\delta^{18}O$, blue line[72]; h. Soreq cave $\delta^{18}O$, brown line[19]).