nature ecology & evolution

ARTICLES

https://doi.org/10.1038/s41559-019-0900-8

Strontium and stable isotope evidence of human mobility strategies across the Last Glacial Maximum in southern Italy

Federico Lugli[1,2*], Anna Cipriani[2,3,10], Giulia Capecchi[4], Stefano Ricci[4], Francesco Boschin[4], Paolo Boscato[4], Paola Iacumin[5], Federica Badino[1,6], Marcello A. Mannino[7,8], Sahra Talamo[8], Michael P. Richards[8,9], Stefano Benazzi[1,8,10] and Annamaria Ronchitelli[4,10]

Understanding the reason(s) behind changes in human mobility strategies through space and time is a major challenge in palaeoanthropology. Most of the time this is due to the lack of suitable temporal sequences of human skeletal specimens during critical climatic or cultural shifts. Here, we present temporal variations in the Sr isotope composition of 14 human deciduous teeth and the N and C stable isotope ratios of four human remains from the Grotta Paglicci site (Apulia, southern Italy). The specimens were recovered from the Gravettian and Epigravettian layers, across the Last Glacial Maximum, and dated between 31210–33103 and 18334–19860 yr cal BP (2σ). The two groups of individuals exhibit different $^{87}Sr/^{86}Sr$ ratios and, while the Gravettians are similar to the local macro-fauna in terms of Sr isotopic signal, the Epigravettians are shifted towards higher radiogenic Sr ratios. These data, together with stable isotopes, can be explained by the adoption of different mobility strategies between the two groups, with the Gravettians exploiting logistical mobility strategies and the Epigravettians applying residential mobility.

People have moved across the landscape since the rise of human species, primarily in search of food[1] but also forced by natural disasters[2], environmental changes[3–6], human conflicts[7] or, more simply, in search of better fortune[8]. Undoubtedly climate change is one of the main reasons behind large-scale human mobility[9,10]. In contrast, small-scale human mobility strategies are related to a mix of different biological and cultural factors that range from the spatial dispersion of local resources[8] to population dynamics[5]. Because moving is bioenergetically expensive, human groups reduce their mobility to a minimum threshold by natural selection, with progressively shorter distances and fewer residential moves per year[11]. In this sense, the reconstruction of hunter-gatherer mobility patterns is a key point in understanding how human activities have been influenced by climate and, in general, in gaining further insight into human mental flexibility during recent evolution.

Two different models describe mobility strategies of modern hunter-gatherer groups in terms of the food–consumer relationship[12]. According to Binford[12], foragers usually do not store food, practising frequent residential moves from their base-camp to the food-resource locus. Collectors, instead, store food and move to key food sites with frequent and targeted logistical forays by a few individuals.

A crucial period in terms of both human mobility and climatic change is represented by the transition from the Gravettian to the later techno-complexes during the Upper Palaeolithic. The Gravettians spread to most of Europe between ~30,000 and ~20,000 years ago and disappeared across the Last Glacial Maximum (LGM), replaced by other complexes—for example, the Italian Epigravettian and the French Iberian Solutrean. Nevertheless, the relationship between the Gravettian and later techno-complexes is unclear (ref. [13] and references therein). Recent ancient DNA analyses associate Epigravettians with the Villabruna genetic Cluster. The latter has affinities with the Near East peoples, suggesting that Gravettians were rapidly substituted by groups migrating from southeastern European/west Asia refugia after the LGM peak[14].

To date, most research on Upper Palaeolithic human mobility has focused on indirect evidence such as raw material procurement (for example, refs. [15–18]), lower limb morphology (for example, refs. [19–22]) and zooarchaeological interpretations (for example, refs. [23,24]). What emerges from these studies is that Gravettian groups relied on large territories covered by long-distance logistical forays, and based their subsistence on a wide variety of food resources on a seasonal basis[16]. Skeletal evidence from limbs appears to indicate the existence within Gravettian groups of a clear division of labour between males and females[20,21] and a high degree of mobility, which decreased during the onset of the LGM[19,22].

In the past two decades, human provenance and mobility studies have benefited from the use of isotopic tracers and the application of the micro-destructive laser ablation multi-collector inductively coupled plasma source mass spectrometry technique[25–29]. This is particularly true for the $^{87}Sr/^{86}Sr$ ratio of dental remains, thanks to the robust relationship of the dental Sr isotope fingerprint with the geographical provenance of the individual (see ref. [30]).

---

[1]Department of Cultural Heritage, University of Bologna, Ravenna, Italy. [2]Department of Chemical and Geological Sciences, University of Modena and Reggio Emilia, Modena, Italy. [3]Lamont-Doherty Earth Observatory, Columbia University, Palisades, NY, USA. [4]Dipartimento di Scienze Fisiche, della Terra e dell'Ambiente, Unità di Ricerca Preistoria e Antropologia, Università degli Studi di Siena, Siena, Italy. [5]Department of Chemistry, Life Sciences and Environmental Sustainability, University of Parma, Parma, Italy. [6]Laboratory of Palynology and Palaeoecology, Istituto per la Dinamica dei Processi Ambientali – CNR, Milan, Italy. [7]Department of Archaeology and Heritage Studies, School of Culture and Society, Aarhus University, Højbjerg, Denmark. [8]Department of Human Evolution, Max Planck Institute for Evolutionary Anthropology, Leipzig, Germany. [9]Department of Archaeology, Simon Fraser University, Burnaby, British Columbia, Canada. [10]These authors jointly supervised this work: Anna Cipriani, Stefano Benazzi, Annamaria Ronchitelli. *e-mail: federico.lugli6@unibo.it

Table 1 | Strontium isotope composition of the local baseline at Grotta Paglicci

Sample	Species	Average $^{87}Sr/^{86}Sr$	2σ	Max. $^{87}Sr/^{86}Sr$	Min. $^{87}Sr/^{86}Sr$	*n*
Macro-mammals	*Equus ferus*	0.70854	0.00028	0.70868	0.70813	30
	Equus hydruntinus	0.70861	0.00025	0.70881	0.70842	10
	Capra ibex	0.70856	0.00014	0.70863	0.70831	29
Rodents	*Microtinae* indet.	0.70842	0.00016	0.70857	0.70826	16
Modern plants	n.d.	0.70846	0.00043	0.70898	0.70813	27

Max., maximum; Min., minimum; n.d., not determined.; indet., species indeterminabilis.

In this paper, we use Sr isotopes of human remains from Grotta Paglicci (Rignano Garganico, Apulia, southern Italy) to assess potential differences in human mobility patterns between Gravettians and Epigravettians. The stratigraphy of the site, located at the foothills of the Gargano promontory, has yielded more than 140 human remains spanning the Early to the Final Epigravettian period and attesting to frequent human use of the area[31,32].

Acting as a sort of climate refugium (for example, refs. [32,33]), Paglicci can be considered an ideal base-camp for hunter-gatherer groups. We therefore analysed the Sr isotopes of 14 human deciduous teeth recovered from the Gravettian (11 teeth) and the Epigravettian (3 teeth) layers of the site, dated between 31210–33103 and 18334–19860 yr BP (2σ) (see Supplementary Table 1 and ref. [32]). Given that the Sr isotope composition of a deciduous tooth reflects that of the mother of the individual (see Supplementary Fig. 1 and ref. [29]), we investigated the mobility of human groups and ultimately the role of women within social dynamics. Moreover, we explored their eating habits utilizing $\delta^{13}C$ and $\delta^{15}N$ of human bone collagen and discuss human behaviour and hunting choices across the LGM in southern Italy.

Results

Sr isotopes. The local baseline of Grotta Paglicci was determined through the analysis of modern plants and rodent teeth. The tooth enamel of several macro-mammals was also analysed for comparison. Considering all the local proxies, a range of $^{87}Sr/^{86}Sr$ ratio between 0.7080 and 0.7088 can be conservatively considered as the broadest and most likely local Sr isotope range. Macro-mammals exhibit the lowest $^{87}Sr/^{86}Sr$ ratio during the Early Gravettian (~0.7081) (Table 1).

In situ laser ablation $^{87}Sr/^{86}Sr$ ratios of 61 enamel micro-samples from 14 human teeth vary between 0.70738 and 0.70952. Considering the average value of each tooth, these ratios range from 0.70800 to 0.70930 (mean, 0.70861 ± 0.00087, 2σ $n = 14$). Statistically significant difference is observed when human isotope data are compared in terms of archaeological period (one-way analysis of variance $n = 61$; $F = 20.3$; $P < 0.00001$; Epigravettian, 0.70926 ± 0.00031; Final Gravettian, 0.70890 ± 0.00066; Evolved Gravettian, 0.70847 ± 0.00085; Early Gravettian, 0.70808 ± 0.00078; Supplementary Fig. 5), with the Epigravettians characterized by the highest radiogenic values and the Early Gravettians by the lowest (Table 2). In terms of temporal evolution, human Sr isotopes increase with time from the Early Gravettian to the Epigravettian (Fig. 1). The more radiogenic $^{87}Sr/^{86}Sr$ ratios of the Epigravettian humans, however, are not paralleled by their respective contemporary fauna which, instead, displays the same values as the late stage of the Gravettian period.

When taking into account the average $^{87}Sr/^{86}Sr$ ratio of each tooth, all but one Gravettian specimen (PA91, $^{87}Sr/^{86}Sr = 0.70900$, Final Gravettian) fit the local bio-available Sr isotope baseline whilst the three Epigravettians exhibit a probable non-local signal (Epigravettians versus rodent teeth; two-tailed Mann–Whitney *U*-test, $P < 0.001$).

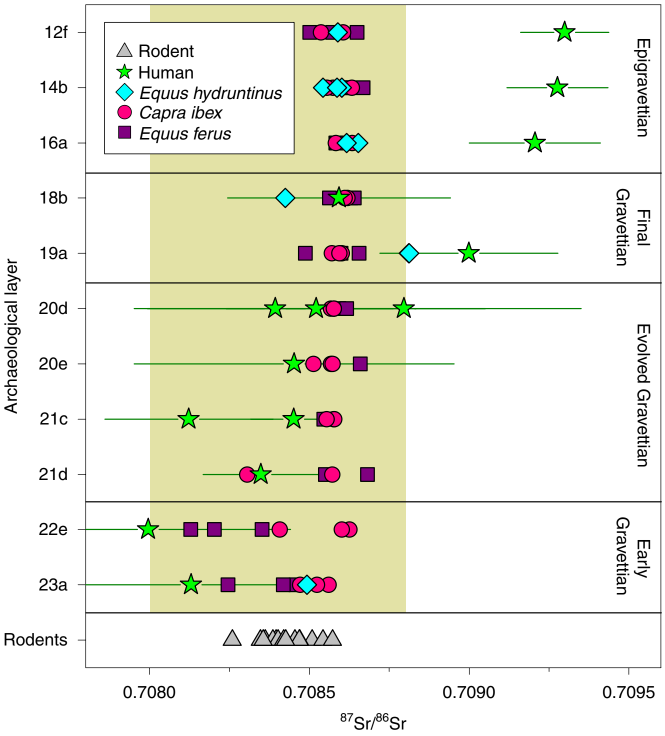

Fig. 1 | Sr isotope ratios of Grotta Paglicci human teeth, with relative stratigraphic positions. Mammals from each layer are also reported for comparison. The shaded area is the local Sr isotope range. Error bars are 1σ.

In terms of intra-tooth variability, expressed as two standard deviations, the Gravettian teeth are very different from the Epigravettian teeth. In general, Epigravettians show limited intra-tooth variation (0.00028–0.00041) whilst the largest intra-tooth variations are observed for Gravettians (0.00027–0.00111). Of the three Gravettian teeth with probable non-local Sr isotope ratios (single laser ablation values), two specimens (PA91 and PA94) show an increase in $^{87}Sr/^{86}Sr$ ratio from the tooth apex to the cervix, with the higher radiogenic values near the cervix; the third tooth (PA93) shows a change in the opposite direction. Despite these fluctuations, all Gravettian teeth possess at least one $^{87}Sr/^{86}Sr$ ratio compatible with the local baseline.

Stable isotopes of bone collagen. The Gravettian human remains Paglicci 12 and Paglicci 25 have $\delta^{13}C$ values of –18.8 and –18.4‰ and $\delta^{15}N$ values of 13.9 and 13‰, respectively.

The $\delta^{13}C$ values of the collagen extracted from Epigravettian human remains are 019.4‰ for PA85 (layers 10–14) and −18.6‰ for PA89 (layer 16b), while $\delta^{15}N$ values are 11 and 14‰, respectively.

We used the data generated by Iacumin et al.[34] on non-ultra-filtered ‘collagen’ as a baseline for interpreting the $\delta^{15}N$ and $\delta^{13}C$

Table 2 | Strontium isotope data from human deciduous teeth from Grotta Paglicci

Techno-complex	Layer	Sample	Tooth element[a,b]	Crown formation (months)	^{88}Sr (V)[c]	Avg ^{87}Sr/^{86}Sr	2σ	Analyses per tooth	Avg ^{87}Sr/^{86}Sr for the period[d]
Early Epigravettian	12f	PA82	Ldi^2	−5 to 2.5	0.53	0.70930	0.00028	3	0.70926
	14	PA83	Ldi^2	−5 to 2.5	0.58	0.70928	0.00032	4	
	16a	PA87	Rdm^1	−5 to 6	0.65	0.70921	0.00041	3	
Final Gravettian	18b	PA90	di(?)	−5 to 2	0.54	0.70859	0.00070	2	0.70890
	19a	PA91	Rdm^1	−5 to 6	1.01	0.70900	0.00056	6	
Evolved Gravettian	20d	PA92	Rdm^1	−5 to 6	0.53	0.70852	0.00106	2	0.70847
	20d	PA93	Rdm_1	−5 to 5.5	0.58	0.70839	0.00088	6	
	20d	PA94	Ldm_1	−5 to 5.5	0.89	0.70880	0.00111	7	
	20e	PA95	di^1	−5.5 to 1.5	0.66	0.70845	0.00100	4	
	21c	PA111	Ldi^1	−5.5 to 1.5	0.72	0.70845	0.00027	5	
	21c	PA112	Ldc_*	−5 to 9	0.53	0.70812	0.00053	4	
	21d	PA40	Rdm_2	−4.5 to 10	0.55	0.70835	0.00036	4	
Early Gravettian	22e	PA129	Ldc^*	−5 to 9	0.67	0.70800	0.00089	4	0.70808
	23a	PA130	Ldi_1	−5.5 to 2.5	0.60	0.70813	0.00077	7	

The approximate crown formation timings are from ref. [67]. [a]L and R indicate left or right, respectively; di, dc and dm denote deciduous incisor, canine and molar, respectively; superscript/subscript numbers and positions indicate the tooth class and upper/lower, respectively (for example, Rdm^1 is the deciduous right upper first molar); [b]position of superscript or subscript indicates upper or lower, respectively; [c]V means volt; [d]mean Sr isotope values for the different periods are calculated from single laser ablation micro-samples reported in Supplementary Table 4.

values of humans from Grotta Paglicci (Fig. 2). The Gravettian humans Paglicci 12 and Paglicci 25 have higher δ^{13}C values (respectively by 1.4–2.1 and 1.8–2.5‰) and δ^{15}N values (respectively by 6.0–7.4 and 5.1–6.5‰) than the mean isotopic ratios for the three terrestrial herbivore species[34]. For the Epigravettian humans, PA85 shows a δ^{15}N value 4.5‰ higher than *Cervus elaphus*, 3.1‰ higher than *Bos primigenius* and 4.2‰ higher than *Equus ferus*; PA89 retains a δ^{15}N value 7.5‰ higher than *C. elaphus*, 6.1‰ higher than *B. primigenius* and 7.2‰ higher than *E. ferus*[34].

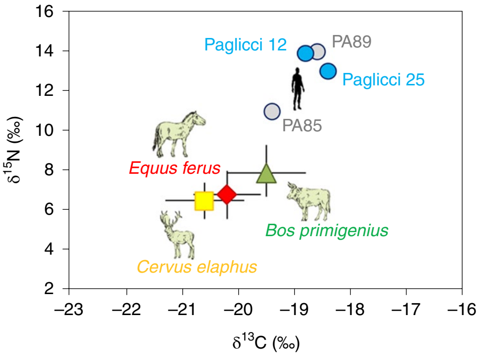

Fig. 2 | Bone collagen N and C stable isotopes of four humans from Grotta Paglicci (filled circles). PA85 and PA89 are Epigravettians; Paglicci 12 and Paglicci 25 are Gravettians. Fauna samples (different symbols colour-coded with the corresponding specific name shown in the Figure) are mean values ±1σ from ref. [34]. The summary statistics for the three main macro-mammal species throughout the Paglicci sequence are as follows: *C. elaphus* (δ^{13}C, range −22.4 to −19.8‰, mean −20.6 ± 0.7‰ δ^{15}N, range 5.0 to 8.5‰, mean 6.5 ± 0.9‰); *B. primigenius* (δ^{13}C, range −20.9 to −17.8‰, mean -19.5 ± 0.7‰ δ^{15}N, range 6.1 to 11.9‰, mean 7.9 ± 1.4‰); *E. ferus* (δ^{13}C, range −21.3 to −19.1‰, mean -20.2 ± 0.6‰ δ^{15}N, range 4.3 to 8.4‰, mean 6.8 ± 1.2‰).

Discussion

Gravettian. The average Sr isotope ratios of all Gravettian teeth, except one (PA91, Final Gravettian), are consistent with the local isotope baseline (0.7080–0.7088). This may simply suggest that the mothers (see Supplementary Fig. 1 and ref. [29]) of these individuals spent most of their pregnancy/breastfeeding period at Grotta Paglicci or at a site with a similar local isotope ratio. Conversely, specimen PA91 displays an average ^{87}Sr/^{86}Sr ratio slightly more radiogenic (0.70900) than the local baseline. In this case, the woman may have spent part of the pregnancy/breastfeeding at a different site or consuming non-local food.

When looking at intra-tooth variability, the Gravettian teeth present very large variability compared to the Epigravettian teeth. Intra-tooth variations may be indicative of the adopted mobility strategies, where a larger isotopic range could be explained by a broader exploitation of patchily distributed resources while a limited intra-tooth range could be interpreted as a narrower territorial utilization or the use of resources from an area with the same local geology. In this sense, we suggest that the larger intra-tooth range observed for some Gravettian individuals may have resulted from sub-annual movements between at least two geologically different places.

The exact source of the Gravettian non-local signals is hard to pinpoint. Modern plant specimens around the site (up to a radius of 20 km) do not have Sr isotope ratios higher than ~0.709 or as low as ~0.707 (Fig. 3). In terms of isotope variability, southern Italy exhibits a narrow ^{87}Sr/^{86}Sr range (~0.707 to ~0.709; refs. [35–37]) because it is mostly dominated by recent limestones ranging in age from the Pliocene to the Quaternary. In this area, isotopic values higher than those of modern seawater (~0.7092) are scarcely documented and are restricted to specific geological areas that include the volcanic area of Roccamonfina and the Hercynian basement outcrops of Calabria and of the easternmost portion of Sicily (^{87}Sr/^{86}Sr ratios up to ~0.71; refs. [35,36]). Instead, low Sr isotope ratios are common among the Campanian, Aeolian and Etna volcanoes[37] and along the Salentine coast[38,39]. Therefore, the higher and lower Sr isotope ratio end-members found in Gravettian teeth could have arisen from the exploitation of resources as far south as, for example, Calabria. Given that values between 0.709 and 0.710 are quite common in other areas of Europe, we cannot precisely identify potential origins from outside Italy. However, archaeological evidence

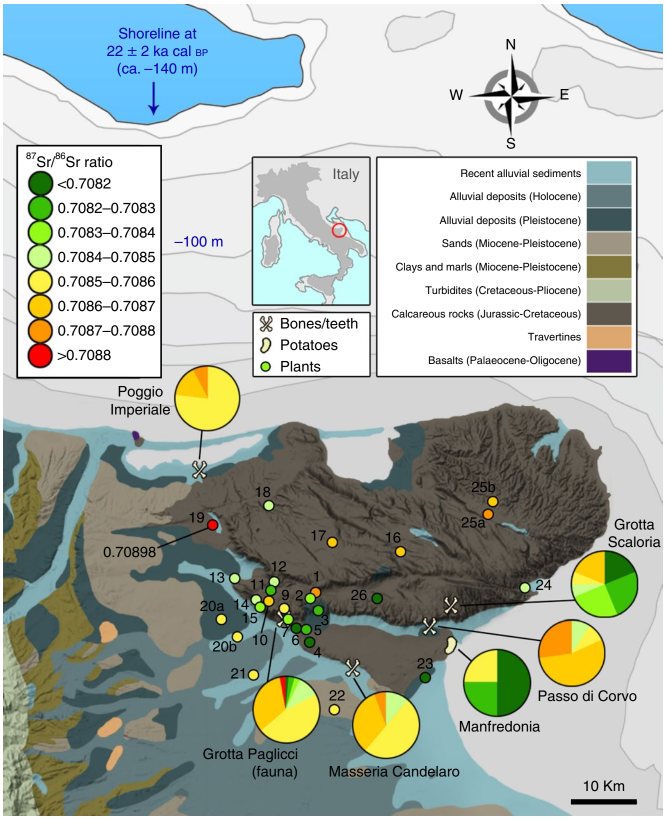

Fig. 3 | Simplified geological map of the surroundings of Grotta Paglicci (location No. 7). The locations of the modern plant sampling sites are numbered and colour-coded based on the average Sr isotope ratio of plants. Pie charts indicate the different proportions of Sr isotope ratios of plants and bone/tooth samples from specific sites. The pie chart Grotta Paglicci depicts the Sr isotope proportion of the fauna enamel samples. The sites Poggio Imperiale, Grotta Scaloria, Passo di Corvo and Masseria Candelaro include bone and tooth Sr isotope ratios sourced from ref. [68]. The Manfredonia site includes data on potatoes from ref. [39].

(Final Epigravettian) indicates the presence in Dalmatia (Kopačina Cave) of raw materials from the Gargano area[40], probably suggesting the possibility of exchanges/contacts with groups from the Balkans.

A more conservative and alternative explanation for Gravettian human Sr isotopes having shifted toward modern seawater (~0.7092) may be the heavy reliance on marine food[41,42] and, therefore, travels towards the Adriatic shore, about 100 km distant at the time.

Taken together, the average local signals registered within Gravettian teeth and the high intra-tooth variability observed for some of these indicate a mobility pattern akin to modern collectors and thus characterized by infrequent base-camp moves and focused logistical forays to gather patchily distributed resources. These mobility strategies are in agreement with the local climatic conditions. As recently suggested by analysis of the micro-fauna from Grotta Paglicci, the climate during the Gravettian was characterized by mean temperatures ~5 °C lower than those of the present day, and by open environments with dry meadows[32]. The coldest conditions, probably correlated to the LGM peak, are found at the end of the Evolved Gravettian (around level 20e). Samples from this time-span are characterized by the highest isotopic intra-tooth variability, suggesting long logistical travels within a period of ~1 year. Ethnographic studies indicate that, in cold environments, modern hunter-gatherers tend to reduce to a minimum residential moves that are highly demanding energetically, but that they exploit targeted forays to collect distant resources (for example, up to 70 km for the Nunamiut[43]). In addition, recent studies on the territorial size of Gravettian groups from Tuscany (Italy) support the hypothesis of major use of the landscape (almost all of Tuscany), with long seasonal logistic travels[16]. Long, targeted forays of the Grotta Paglicci Gravettian humans are also evidenced by the presence of ornamental seashells from one of the buried individuals (Paglicci 25, level 21b; ref. [31]) and by the presence of marine gastropods along the archaeological sequence, which suggests that Gravettians walked at least ~100 km to gather shells from the Adriatic shore.

Nevertheless, no evidence for these movements is found within the macro-fauna isotopic record. However, the homogeneous geology of central Italian bedrock (limestones dating between Jurassic and Holocene) most probably masks the high-mobility patterns of fauna[44].

From our Sr data, we can cautiously speculate that humans from Grotta Paglicci in the Gravettian exploited local fauna, at least seasonally, perhaps following the annual movements of ungulates. This is evident especially during the Early Gravettian, when the Sr isotope ratios of both humans and animals tend to converge towards a common lower value, with *E. ferus* the lowest and most likely isotopic end-member. This low ratio within the considered fauna is consistent with animal movements/migrations toward the southern portion of the Apulia region[39]. Zooarchaeological and taphonomic evidence of the earliest stages of the Gravettian also suggests also a strong reliance on ungulates from open habitats[45].

Stable isotopes of carbon and nitrogen support the idea of a high-protein diet for the two buried Gravettian individuals studied (Paglicci 12 and Paglicci 25). Given that their isotope composition was enriched by more than one trophic step ($\delta^{13}C \approx 1.0‰$ $\delta^{15}N = 3.0\text{–}5.0‰$) compared to some of their main terrestrial prey, these individuals probably relied on meat from large-sized mammals with the additional limited intake of a secondary protein source. $\delta^{13}C$ values higher than $-18.8‰$ and $\delta^{15}N$ values higher than 13‰ are compatible with the consumption of aquatic resources, as observed for other Upper Palaeolithic humans (for example, refs. [46–48]), possibly exploited on a seasonal basis (Fig. 2). While fish remains are absent at Grotta Paglicci, bird bones with butchering marks are present within the Early Gravettian layers, thus indicating a possible minimal consumption of freshwater birds[49]. Nevertheless, high-protein diets may isotopically mask the intake of resources from low trophic levels, such as the use of plant foods. Recent residue analyses of a grinding tool from the Early Gravettian layer 23a of Grotta Paglicci support the processing and exploitation of flours by humans[50]. Such a wide dietary breadth, though based largel on fauna exploitation, is in agreement with the logistical mobility model we defined for the Gravettians of Grotta Paglicci based on Sr isotopes. In fact modern hunter-gatherers, heavily reliant on faunal resources, may use a large territorial range during the year but they do not necessarily practise residential moves as frequently as do groups that are dependent on plant gathering[51]. Within societies living in cold environments, men alone fulfill the dietary requirement of the group with the procurement of large game. Women are generally taking care of children and/or foraging for local plants, limited in terms of long-distance mobility by the burden of pregnancy[52]. Hence it is not unlikely that, within Gravettian groups, labour tasks were divided between men and women[21,22] perhaps driven by seasons and the dietary requirements of the entire group. Although not entirely supported by stable isotopes, the more radiogenic Sr values in some human dental enamel, not far from the modern seawater value (~0.7092), may have resulted from periodic travels to the seashore. The exploitation of molluscs as food by Late Pleistocene groups has been demonstrated within other coastal regions of the Italian landscape—for example, Liguria (Riparo Mochi and Arene Candide[53]).

Epigravettian. Sr isotopes of human enamel indicate that Epigravettians from Grotta Paglicci based their subsistence mostly

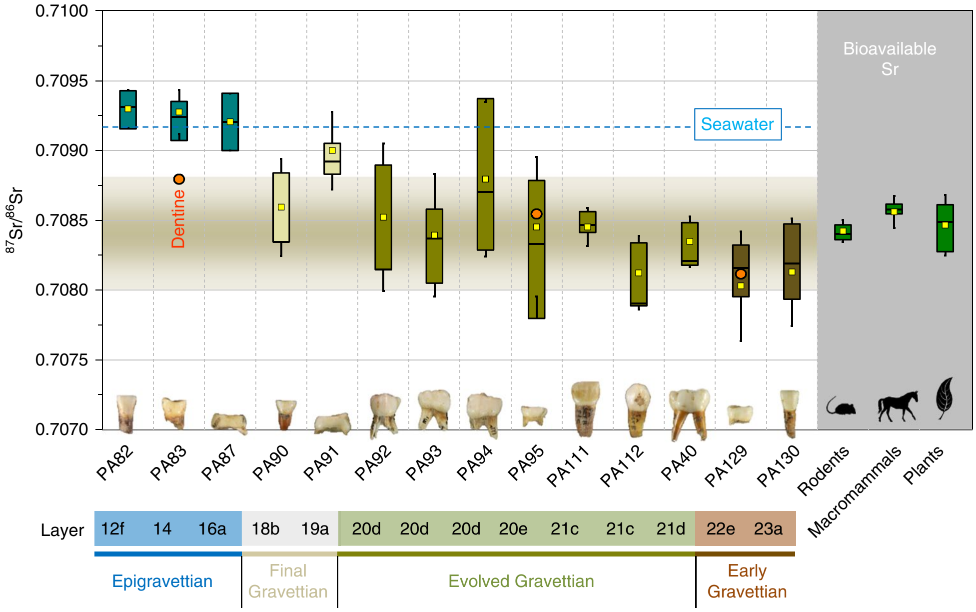

Fig. 4 | Sr isotope ratios of human deciduous teeth from Grotta Paglicci. Bio-available Sr isotope ratios are reported for comparison. A cut-off value of 0.7088 is set as the maximum value for the local isotope baseline. Box plot bars are 1σ.

on non-local resources, with their isotope ratio being more radiogenic than the local bio-available Sr. Thus, as deciduous teeth grew, it is likely that the mothers of these individuals may have lived for 6–12 months in a place not identifiable with the surroundings of Grotta Paglicci. Moreover, the very limited intra-tooth variability of Epigravettian teeth (0.0003–0.0004, see Fig. 4) suggests that, during this period, mothers did not move much, residing in the same place or moving across areas with the same isotopic ratio (>0.709). Given that these teeth derive from different archaeological layers, their non-local isotopic ratio should reflect a type of recurring mobility pattern, possibly constrained by seasons and consistent with the residential mobility model[12]. According to this model, modern foragers gather resources near the base-camp but, when resources begin to run out, the base-camp is moved. A diet including small mammals or plants, rather than large game, is also more likely in gathering economies because foraging at short distances from the base-camp allows the use of low-return rate resources[51]. However, during this period we have no evidence from Grotta Paglicci of a strong dependency on small mammals in terms of zooarchaeological records[45].

Lithic data from Apulia[54,55] appear to suggest a change in terms of human mobility across the LGM. This has been interpreted to indicate the exploitation of logistical mobility by Epigravettian groups rather than residential[54,55], in contrast to what we propose based on Sr isotopes. However, we stress that, while our human specimens are from the Early Epigravettian, the lithic assemblages from refs. [54,55] are much younger (5–10 ka). This might suggest a long-term adaptation of the Epigrattevians to the local environment and a consequent change in their mobility patterns.

Stable isotopes show that the diet of the two Epigravettian individuals was based mainly on terrestrial resources. However, while PA89 shows a high-protein diet in line with Gravettians, with a scarce (or masked) intake of plant foods and limited use of aquatic resources, PA85 retains a lighter nitrogen isotope fingerprint suggesting a more balanced omnivorous diet, with the consumption of both meat and plants. The probable higher consumption of low-trophic level resources by PA85 matches the foraging model proposed here for the Epigravettians. Given the diverging Sr isotope ratios of fauna and humans, we infer that the Epigravettians from Grotta Paglicci exploited local macro-mammals less intensively. This, however, does not exclude the consumption of large game meat but suggests the intake of non-local meat as seasonal or annual resource. Altogether, this evidence supports variation in mobility pattern between Epigravettians and Gravettians. Residential moves were the main system used to tackle resources for Epigravettians, similarly to modern foragers.

Another possible explanation for the recurring non-local values of Epigravettians can be found in birth seasonality. Among the !Kung forager tribe of the Kalahari desert, conceptions are concentrated between June and August when the highest amount of food is available and the season allows the least expenditure of energy[56]. Assuming that moves of the base-camp during the Epigravettian were on a seasonal basis, we can prudently put forward the hypothesis that the three children studied here were born non-locally, possibly during favourable seasons. As the climate deteriorated and/or food resources ran out, the human group might have moved camp to Grotta Paglicci in search of new resources or better living conditions. Nevertheless, our inferences are constrained by the limited number of human specimens at our disposal from the Epigravettian layers.

Is change in mobility strategies driven by climate or culture?.

Although a gradual climatic change has been detected globally across the LGM (from GS3 to GS2; ref. [57]), local palaeoclimate proxies do not record strong modifications of the environment at Grotta Paglicci during the transition from the Gravettian to the Early Epigravettian within the time-span covered by the human specimens of this study[45,58]. The persistence of cold steppe vegetation indicates a predominance of at least seasonally dry conditions, although with short intervals of woodland expansion. Moreover, micro-mammal remains suggest the start of a gradual climatic improvement at the onset of the Early Epigravettian, ending with a shift to a Mediterranean climate during the late phases of the Epigravettian[32].

Given the probable lack of an evident local and regional environmental change at Grotta Paglicci, we cannot be certain that climate influenced the human mobility change recorded by our data. Nevertheless, the presence of phases with stands of open coniferous woodland developed in favourable areas of the landscape may have pushed humans to change their mobility patterns to adapt to the new environmental conditions[51].

We thus cautiously propose that the different mobility patterns observed in the Gravettian–Epigravettian transition of Paglicci might be related to cultural factors, which in turn may be indicative of a population replacement during the Epigravettian. This hypothesis agrees with genetic data[13,14] and also with the probable change in hunting strategies as shown by the lithic and bone industries of Grotta Paglicci[59]. In particular, we observe a marked difference at the transition between the two techno-complexes in the lithic industry, with a substantial size increase during the Epigravettian and a concurrent disappearance of the small curved points, typical of the Paglicci final Gravettian[59]. Moreover, during the Early Epigravettian a change in hunting strategies is also reflected by the strong presence of antler spearpoints and shouldered stone points, correlated with a faunal assemblage mostly dominated by remains of *C. ibex*[60]. A population discontinuity hypothesis at the onset of the LGM was also put forward by Brewster et al.[61], based on the analysis of cranial morphology. Here the authors found a strong statistical separation between pre-LGM and later human groups, suggesting population dynamics as the main cause of this divergent pattern.

Finally, we speculate that global climate improvement might have facilitated the arrival of new groups of people from the north or east, driven by the general environment amelioration and the opening up of new corridors.

Methods

Detailed methodological protocols are reported within the Supplementary Information.

Sr isotopes. Fourteen human deciduous teeth (six incisors, two canines and six molars, see Table 2) from Grotta Paglicci were considered in this study (Supplementary Fig. 6). Specimens PA92, PA93 and PA94 were recovered from the same archaeological layer (20d) and could have belonged to the same individual. Similarly, also PA111 and PA112 came from the same archaeological layer (21c) (see Supplementary Information for further details and Supplementary Table 5). The $^{87}Sr/^{86}Sr$ ratios of all teeth were measured in situ with a multi-collector inductively coupled plasma mass spectrometer (MC–ICP–MS; Neptune (ThermoFisher Scientific)) coupled to a 213 nm laser ablation system (New Wave Research) housed at the Centro Interdipartimentale Grandi Strumenti of the University of Modena and Reggio Emilia, following protocols described in Lugli et al[35]. Rodent ($n=16$) and macro-mammal ($n=69$) teeth were collected from the layers of Grotta Paglicci according to the chronological distribution of human samples. Modern plants were sampled in the area surrounding Grotta Paglicci, and each specimen is a pool of different arboreal plants grown in natural areas away from roads and cultivated fields (Supplementary Table 2). Fauna and plant specimens were analysed by solution MC–ICP–MS following the chemical separation of Sr[29].

Carbon and nitrogen stable isotopes of bone collagen. The bone pretreatment method used for the two Gravettian individuals (Paglicci 12 and Paglicci 25) is that established by Talamo and Richards[62] (see also Supplementary Information for further details). The isotope analyses were conducted at the Max Planck Institute for Evolutionary Anthropology in Leipzig, on a Thermo Finnigan Delta V Advantage Isotope Ratio Mass Spectrometer coupled to a Flash 2000 EA. The ulna of Paglicci 12 (S-EVA 28202) and the rib of Paglicci 25 (S-EVA 13777) have extracts compatible with well-preserved collagen[63].

Bone collagen from the Epigravettian human specimens (PA85 and PA89) was extracted at the Stable Isotope Laboratory of the University of Parma, following the protocol described by Longin[64] and modified by Ambrose and Bocherens et al.[65,66]. Carbon and nitrogen ratios were measured by means of a carbon, hydrogen, nitrogen elemental analyser coupled to a mass spectrometer.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

All data generated or analysed during this study are included in this paper and its Supplementary Information files.

Received: 12 October 2018; Accepted: 12 April 2019;

References

1. Kelly, R. L. Mobility/sedentism: concepts, archaeological measures, and effects. *Annu. Rev. Anthropol.* **21**, 43–66 (1992).
2. Hunter, L. M. Migration and environmental hazards. *Popul. Environ.* **26**, 273–302 (2005).
3. Büntgen, U. et al. 2500 years of European climate variability and human susceptibility. *Science* **331**, 578–583 (2011).
4. Kelley, C. P., Mohtadi, S., Cane, M. A., Seager, R. & Kushnir, Y. Climate change in the Fertile Crescent and implications of the recent Syrian drought. *Proc. Natl Acad. Sci. USA* **112**, 3241–3246 (2015).
5. Tallavaara, M., Luoto, M., Korhonen, N., Järvinen, H. & Seppä, H. Human population dynamics in Europe over the Last Glacial Maximum. *Proc. Natl Acad. Sci. USA* **112**, 8232–8237 (2015).
6. Lamb, H. F. et al. 150,000-year palaeoclimate record from northern Ethiopia supports early, multiple dispersals of modern humans from Africa. *Sci. Rep.* **8**, 1077 (2018).
7. Halsall, G. *Barbarian Migrations and the Roman West* 376–568 (Cambridge University Press, 2007).
8. Kuhn, S. L., Raichlen, D. A. & Clark, A. M. Y. E. What moves us? How mobility and movement are at the center of human evolution. *Evol. Anthropol.* **25**, 86–97 (2016).
9. D'Andrea, W. J., Huang, Y., Fritz, S. C. & Anderson, N. J. Abrupt Holocene climate change as an important factor for human migration in west Greenland. *Proc. Natl Acad. Sci. USA* **108**, 9765–9769 (2011).
10. Timmermann, A. & Friedrich, T. Late Pleistocene climate drivers of early human migration. *Nature* **538**, 92–95 (2016).
11. Venkataraman, V. V., Kraft, T. S., Dominy, N. J. & Endicott, K. M. Hunter-gatherer residential mobility and the marginal value of rainforest patches. *Proc. Natl Acad. Sci. USA* **114**, 3097–3102 (2017).
12. Binford, L. R. Willow smoke and dogs' tails: hunter-gatherer settlement systems and archaeological site formation. *Am. Antiq.* **45**, 4–20 (1980).
13. Pala, M. et al. Mitochondrial DNA signals of late glacial recolonization of Europe from Near Eastern refugia. *Am. J. Hum. Genet.* **90**, 915–924 (2012).
14. Fu, Q. et al. The genetic history of Ice Age Europe. *Nature* **534**, 200–205 (2016).
15. Arrizabalaga, A., Calvo, A., Elorrieta, I., Tapia, J. & Tarriño, A. Where to and what for? Mobility patterns and the management of lithic resources by Gravettian hunter-gatherers in the Western Pyrenees. *J. Anthropol. Res.* **70**, 233–261 (2014).
16. Aranguren, B. et al. Territorial exploitation in the Tyrrhenian Gravettian Italy: the case-study of Bilancino (Tuscany). *Quat. Int.* **359–360**, 442–451 (2015).
17. Moreau, L. et al. Geochemical sourcing of flint artifacts from Western Belgium and the German Rhineland: testing hypotheses on Gravettian period mobility and raw material economy. *Geoarchaeology* **31**, 229–243 (2016).
18. Tomasso, A. & Porraz, G. Hunter-gatherer mobility and embedded raw-material procurement strategies in the Mediterranean Upper Paleolithic. *Evol. Anthropol.* **25**, 164–174 (2016).
19. Holt, B. M. Mobility in Upper Paleolithic and Mesolithic Europe: evidence from the lower limb. *Am. J. Phys. Anthropol.* **122**, 200–215 (2003).
20. Villotte, S., Samsel, M. & Sparacello, V. The paleobiology of two adult skeletons from Baousso da Torre (Bausu da Ture) (Liguria, Italy): implications for Gravettian lifestyle. *C. R. Palevol.* **16**, 462–473 (2017).
21. Villotte, S., Churchill, S. E., Dutour, O. J. & Henry-Gambier, D. Subsistence activities and the sexual division of labor in the European Upper Paleolithic and Mesolithic: evidence from upper limb enthesopathies. *J. Hum. Evol.* **59**, 35–43 (2010).
22. Holt, B. M. & Formicola, V. Hunters of the Ice Age: the biology of Upper Paleolithic people. *Am. J. Phys. Anthropol.* **137**(S47), 70–99 (2008).
23. Boscato, P. Faunes gravettiennes à grands mammifères de l'Italie du Sud: Grotta della Cala (Salerno) et Grotta Paglicci (Foggia). *Paleo* **19**, 109–114 (2007).
24. Tagliacozzo, A., Zeppieri, F., Fiore, I., Spinapolice, E. & Del Lucchese, A. Archaeozoological evidence of subsistence strategies during the Gravettian at Riparo Mochi (Balzi Rossi, Ventimiglia, Imperia – Italy). *Quat. Int.* **252**, 142–154 (2012).
25. Richards, M. et al. Strontium isotope evidence of Neanderthal mobility at the site of Lakonis, Greece using laser-ablation PIMMS. *J. Archaeol. Sci.* **35**, 1251–1256 (2008).
26. Willmes, M. et al. Improvement of laser ablation in situ micro-analysis to identify diagenetic alteration and measure strontium isotope ratios in fossil human teeth. *J. Archaeol. Sci.* **70**, 102–116 (2016).
27. Copeland, S. R. et al. Strontium isotope evidence for landscape use by early hominins. *Nature* **474**, 76–78 (2011).
28. Balter, V., Braga, J., Télouk, P. & Thackeray, J. F. Evidence for dietary change but not landscape use in South African early hominins. *Nature* **489**, 558–560 (2012).
29. Lugli, F. et al. Suspected limited mobility of a Middle Pleistocene woman from southern Italy: strontium isotopes of a human deciduous tooth. *Sci. Rep.* **7**, 8615 (2017).

30. Bentley, R. A. Strontium isotopes from the earth to the archaeological skeleton: a review. *J. Archaeol. Method Theory* **13**, 135–187 (2006).
31. Ronchitelli, A. et al. When technology joins symbolic behaviour: the Gravettian burials at Grotta Paglicci (Rignano Garganico e Foggia e Southern Italy). *Quat. Int.* **359**, 423–441 (2015).
32. Berto, C., Boscato, P., Boschin, F., Luzi, E. & Ronchitelli, A. Paleoenvironmental and paleoclimatic context during the Upper Palaeolithic (late Upper Pleistocene) in the Italian Peninsula. The small mammal record from Grotta Paglicci (Rignano Garganico, Foggia, Southern Italy). *Quat. Sci. Rev.* **168**, 30–41 (2017).
33. Sommer, R. S. & Nadachowski, A. Glacial refugia of mammals in Europe: evidence from fossil records. *Mammal. Rev.* **36**, 251–265 (2006).
34. Iacumin, P., Bocherens, H., Huertas, A. D., Mariotti, A. & Longinelli, A. A stable isotope study of fossil mammal remains from the Paglicci cave, Southern Italy: N and C as palaeoenvironmental indicators. *Earth Planet. Sci. Lett.* **148**, 349–357 (1997).
35. Lugli, F., Cipriani, A., Peretto, C., Mazzucchelli, M. & Brunelli, D. In situ high spatial resolution ^{87}Sr/^{86}Sr ratio determination of two Middle Pleistocene (ca 580 ka) *Stephanorhinus hundsheimensis* teeth by LA–MC–ICP–MS. *Int. J. Mass Spectrom.* **412**, 38–48 (2017).
36. Emery, M. V. et al. Mapping the origins of Imperial Roman workers ((1st–4th century CE) at Vagnari, Southern Italy, using ^{87}Sr/^{86}Sr and d^{18}O variability. *Am. J. Phys. Anthropol.* **166**, 837–850 (2018).
37. De Astis, G., Kempton, P. D., Peccerillo, A. & Wu, T. W. Trace element and isotopic variations from Mt. Vulture to Campanian volcanoes: constraints for slab detachment and mantle inflow beneath southern Italy. *Contrib. Mineral Petrol* **151**, 331–351 (2006).
38. Schlüter, M., Steuber, T. & Parente, M. Chronostratigraphy of Campanian–Maastrichtian platform carbonates and rudist associations of Salento (Apulia, Italy). *Cretac. Res.* **29**, 100–114 (2008).
39. Zampella, M. et al. Soil properties, strontium isotopic signatures and multi-element profiles to authenticate the origin of vegetables from small-scale regions: illustration with early potatoes from southern Italy. *Rapid Commun. Mass Spectrom.* **25**, 2721–2731 (2011).
40. Vukosavljević, N. & Perhoč, Z. Lithic raw material procurement of the Late Epigravettian hunter-gatherers from Kopačina Cave (island of Brač, Dalmatia, Croatia). *Quat. Int.* **450**, 164–185 (2017).
41. Montgomery, J., Evans, J. A. & Cooper, R. E. Resolving archaeological populations with Sr-isotope mixing models. *Appl. Geochem.* **22**, 1502–1514 (2007).
42. Frei, K. M. & Price, T. D. Strontium isotopes and human mobility in prehistoric Denmark. *Archaeol. Anthropol. Sci.* **4**, 103–114 (2012).
43. Binford, L. R. Dimensional analysis of behavior and site structure: learning from an Eskimo hunting stand. *Am. Antiq.* **43**, 330–361 (1978).
44. Pellegrini, M. et al. Faunal migration in late-glacial central Italy: implications for human resource exploitation. *Rapid Commun. Mass Spectrom.* **22**, 1714–1726 (2008).
45. Boschin, F., Boscato, P., Berto, C., Crezzini, J. & Ronchitelli, A. The palaeoecological meaning of macromammal remains from archaeological sites exemplified by the case study of Grotta Paglicci (Upper Palaeolithic, Southern Italy). *Quat. Res.* **90**, 470–482 (2018).
46. Richards, M. P., Jacobi, R. M., Cook, J., Pettitt, P. B. & Stringer, C. B. Isotope evidence for the intensive use of marine foods by Late Upper Palaeolithic humans. *J. Hum. Evol.* **49**, 390–394 (2005).
47. Richards, M. P. in *The Evolution of Hominin Diets* (eds Hublin, J. J. & Richards, M. P.) 251–257 (Springer, 2009).
48. Richards, M. P. & Trinkaus, E. Isotopic evidence for the diets of European Neanderthals and early modern humans. *Proc. Natl Acad. Sci. USA* **106**, 16034–16039 (2009).
49. Tagliacozzo A. & Gala M. in *Paglicci, l'Aurignaziano e il Gravettiano antico* (ed. Di Cesnola, P.) 71–89 (Grenzi, 2004).
50. Mariotti Lippi, M., Foggi, B., Aranguren, B., Ronchitelli, A. & Revedin, A. Multistep food plant processing at Grotta Paglicci (Southern Italy) around 32,600 cal BP. *Proc. Natl Acad. Sci. USA* **112**, 12075–12080 (2015).
51. Kelly R. L. *The Foraging Spectrum: Diversity in Hunter-Gatherer Lifeways* (Percheron Press, 2007).
52. Wall-Scheffler, C. M. & Myers, M. J. Reproductive costs for everyone: how female loads impact human mobility strategies. *J. Hum. Evol.* **64**, 448–456 (2013).
53. Colonese, A. C. et al. Marine mollusc exploitation in Mediterranean prehistory: an overview. *Quat. Int.* **239**, 86–103 (2011).
54. Milliken, S. Hunter-gatherer land use in Late Glacial south-east Italy. *Oxford J. Archaeol.* **17**, 269–286 (1998).
55. Riel-Salvatore, J. & Barton, C. M. Late Pleistocene technology, economic behavior, and land-use dynamics in southern Italy. *Am. Antiq.* **69**, 257–274 (2004).
56. Bentley, G. R. Hunter-gatherer energetics and fertility: a reassessment of the !Kung San. *Hum. Ecol.* **13**, 79–107 (1985).
57. Andersen, K. K. et al. The Greenland ice core chronology 2005, 15–42 ka. Part 1: constructing the time scale. *Quat. Sci. Rev.* **25**, 3246–3257 (2006).
58. Allen, J. R. et al. Rapid environmental changes in southern Europe during the last glacial period. *Nature* **400**, 740–743 (1999).
59. Bartolomei, G., Broglio, A. & Palma di Cesnola, A. in *La Fin des Temps Glaciaires en Europe* (ed. de Sonneville-Bordes, D.) 297–324 (Editions du CNRS, 1979).
60. Borgia, V., Boschin, F. & Ronchitelli, A. Bone and antler working at Grotta Paglicci (Rignano Garganico, Foggia, Southern Italy). *Quat. Int.* **403**, 23–39 (2016).
61. Brewster, C., Meiklejohn, C., von Cramon-Taubadel, N. & Pinhasi, R. Craniometric analysis of European Upper Palaeolithic and Mesolithic samples supports discontinuity at the last glacial maximum. *Nat. Commun.* **5**, 4094 (2014).
62. Talamo, S. & Richards, M. A. Comparison of bone pretreatment methods for AMS dating of samples >30,000 bp. *Radiocarbon* **53**, 443–449 (2011).
63. Van Klinken, G. J. Bone collagen quality indicators for palaeodietary and radiocarbon measurements. *J. Archaeol. Sci.* **26**, 687–695 (1999).
64. Longin, R. New method of collagen extraction for radiocarbon dating. *Nature* **230**, 241–242 (1971).
65. Ambrose, S. H. Preparation and characterization of bone and tooth collagen for isotopic analysis. *J. Archaeol. Sci.* **17**, 431–451 (1990).
66. Bocherens, H. et al. Isotopic biogeochemistry (13C, 15N) of fossil vertebrate collagen: implications for the study of fossil food web including Neanderthal Man. *J. Hum. Evol.* **20**, 481–492 (1991).
67. Nelson, S. J. & Ash, M. M. *Wheeler's Dental Anatomy, Physiology, and Occlusion* 9th edn (Elsevier, Saunders, 2010).
68. Tafuri, M. A. et al. Life and death in Neolithic southeastern Italy: the strontium isotopic evidence. *Int. J. Osteoarchaeol.* **26**, 1045–1057 (2016).

Acknowledgements

This project was funded by the European Research Council under the European Union's Horizon 2020 Research and Innovation Programme (grant agreement No. 724046—SUCCESS, awarded to S.B.). The Radiogenic Isotope Laboratory of the University of Modena and Reggio Emilia was funded through a grant from Programma Giovani Ricercatori Rita Levi Montalcini (to A.C.). We thank Soprintendenza Archeologia, Belle Arti e Paesaggio per le Province di Barletta-Andria-Trani e Foggia for supporting researches at Grotta Paglicci, and A. Palma di Cesnola for his scientific rigour in carrying out studies at Grotta Paglicci. The authors acknowledge S. Conti for providing geological maps of the Apulia region and A. Florenzano for valuable discussions of the paleoclimate record.

Author contribution

F.L., A.C. and S.B. conceived the study and designed the experiments. F.L. and A.C. performed the laboratory work and Sr isotope analyses. M.A.M, S.T., P.I. and M.P.R. designed and performed the stable isotope analyses. G.C., S.R., F. Boschin, P.B. and A.R. provided the samples. F. Badino, F. Boschin and P.B. reviewed palaeoclimate data. S.B., A.C. and A.R. supervised the work. All authors contributed to writing the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at https://doi.org/10.1038/s41559-019-0900-8.

Reprints and permissions information is available at www.nature.com/reprints.

Correspondence and requests for materials should be addressed to F.L.

Publisher's note: Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.

nature research

Corresponding author(s): Federico Lugli

Last updated by author(s): Apr 11, 2019

Reporting Summary

Statistics

For all statistical analyses, confirm that the following items are present in the figure legend, table legend, main text, or Methods section.

n/a	Confirmed	
☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒	A statement on whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☒	☐	A description of all covariates tested
☒	☐	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistical parameters including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☒	☐	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☒	☐	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated

Our web collection on statistics for biologists contains articles on many of the points above.

Software and code

Policy information about availability of computer code

Data collection	ThermoFisher software for MC-ICP-MS Neptune
Data analysis	Microsoft Excel, Origin, Matlab

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

All data are provided within the manuscript and the supplementary materials

Field-specific reporting

Please select the one below that is the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/documents/nr-reporting-summary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	Isotope study of human and animal fossil teeth from the Upper Palaeolithic layers of Grotta Paglicci (Apulia, Italy)
Research sample	All the avilable deciduous human teeth from the archeological site were studied. The animal teeth were selected based on the degree of preservation. Modern plants were collected in the surroundings of the archaeological site, covering all the local lithologies.
Sampling strategy	No statistical analyses were used to determine the sample size. A sub-sample of the entire fauna sample (to build the baseline) was selected based on the preservation of the specimens (visual inspection). The sample size of fauna and modern plants was determined based on what is reported in literature.
Data collection	Data were collected by Dr. Federico Lugli during MC-ICP-MS Neptune sessions.
Timing and spatial scale	Isotope data of human teeth were collected during two LA-MC-ICP-MS sessions (6th and 7th February 2017). Fauna specimens were prepared (sample selection, clening, enamel drilling and column chemistry) and analysed during September 2017. Modern plant specimens were collected, prepared and analysed during May 2018.
Data exclusions	No data were excluded from the analysis.
Reproducibility	All attempts to repeat the experiments were successful. Several reference materials were measured during the analyses to check the reproducibility of the measures.
Randomization	Randomization is not relevant in this study.
Blinding	Blinding is not relevant in this study.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	No rainfall occurred during the sampling of modern plant specimens.
Location	Modern plant specimens were collected in the surroundings of the Grotta Paglicci site (Rignano Garganico, Apulia, Italy). Any relevant environmental parameter need to be reported.
Access and import/export	Samples were collected in public properties according to Italian national laws. No need for permits was necessary.
Disturbance	No disturbance was caused during the sampling.

Reporting for specific materials, systems and methods

We require information from authors about some types of materials, experimental systems and methods used in many studies. Here, indicate whether each material, system or method listed is relevant to your study. If you are not sure if a list item applies to your research, read the appropriate section before selecting a response.

Materials & experimental systems

n/a	Involved in the study
☒	☐ Antibodies
☒	☐ Eukaryotic cell lines
☐	☒ Palaeontology
☒	☐ Animals and other organisms
☒	☐ Human research participants
☒	☐ Clinical data

Methods

n/a	Involved in the study
☒	☐ ChIP-seq
☒	☐ Flow cytometry
☒	☐ MRI-based neuroimaging

Palaeontology

Specimen provenance	Samples were collected and analysed according to the current standing agreement between the University of Siena and the Soprintendenza Archeologia, Belle Arti e Paesaggio per le Province di Barletta-Andria-Trani e Foggia.
Specimen deposition	Specimens are currently deposited at the Department of Physical Sciences, Earth and Environment of the University of Siena.

Dating methods	No new dates are reported in this work.

☐ Tick this box to confirm that the raw and calibrated dates are available in the paper or in Supplementary Information.

Nature Research, brought to you courtesy of Springer Nature Limited (“Nature Research”)

Terms and Conditions

Nature Research supports a reasonable amount of sharing of content by authors, subscribers and authorised or authenticated users (“Users”), for small-scale personal, non-commercial use provided that you respect and maintain all copyright, trade and service marks and other proprietary notices. By accessing, viewing or using the nature content you agree to these terms of use (“Terms”). For these purposes, Nature Research considers academic use (by researchers and students) to be non-commercial.

These Terms are supplementary and will apply in addition to any applicable website terms and conditions, a relevant site licence or a personal subscription. These Terms will prevail over any conflict or ambiguity with regards to the terms, a site licence or a personal subscription (to the extent of the conflict or ambiguity only). By sharing, or receiving the content from a shared source, Users agree to be bound by these Terms.

We collect and use personal data to provide access to the nature content. ResearchGate may also use these personal data internally within ResearchGate and share it with Nature Research, in an anonymised way, for purposes of tracking, analysis and reporting. Nature Research will not otherwise disclose your personal data unless we have your permission as detailed in the Privacy Policy.

Users and the recipients of the nature content may not:

1. use the nature content for the purpose of providing other users with access to content on a regular or large scale basis or as a means to circumvent access control;
2. use the nature content where to do so would be considered a criminal or statutory offence in any jurisdiction, or gives rise to civil liability, or is otherwise unlawful;
3. falsely or misleadingly imply or suggest endorsement, approval , sponsorship, or association unless explicitly agreed to by either Nature Research or ResearchGate in writing;
4. use bots or other automated methods to access the nature content or redirect messages; or
5. override any security feature or exclusionary protocol.

These terms of use are reviewed regularly and may be amended at any time. We are not obligated to publish any information or content and may remove it or features or functionality at our sole discretion, at any time with or without notice. We may revoke this licence to you at any time and remove access to any copies of the shared content which have been saved.

Sharing of the nature content may not be done in order to create substitute for our own products or services or a systematic database of our content. Furthermore, we do not allow the creation of a product or service that creates revenue, royalties, rent or income from our content or its inclusion as part of a paid for service or for other commercial gain. Nature content cannot be used for inter-library loans and librarians may not upload nature content on a large scale into their, or any other, institutional repository.

To the fullest extent permitted by law Nature Research makes no warranties, representations or guarantees to Users, either express or implied with respect to the nature content and all parties disclaim and waive any implied warranties or warranties imposed by law, including merchantability or fitness for any particular purpose.

Please note that these rights do not automatically extend to content, data or other material published by Nature Research that we license from third parties.

If you intend to distribute our content to a wider audience on a regular basis or in any other manner not expressly permitted by these Terms please contact us at

onlineservice@springernature.com
The Nature trademark is a registered trademark of Springer Nature Limited.