Dental calculus indicates widespread plant use within the stable Neanderthal dietary niche

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Abstract

The ecology of Neanderthals is a pressing question in the study of hominin evolution. Diet appears to have played a prominent role in their adaptation to

Eurasia. Based on isotope and zooarchaeological studies, Neanderthal diet has been reconstructed as heavily meat-based and generally similar across different environments. This image persists, despite recent studies suggesting more plant use and more variation. However, we have only a fragmentary picture of their dietary ecology, and how it may have varied among habitats, because we lack broad and environmentally representative information about their use of plants and other foods. To address the problem, we examined the plant microremains in Neanderthal dental calculus from five archaeological sites representing a variety of environments from the northern Balkans, and the western, central and eastern Mediterranean. The recovered microremains revealed the consumption of a variety of non-animal foods, including starchy plants. Using a modeling approach, we explored the relationships among microremains and environment, while controlling for chronology. In the process, we compared the effectiveness of various diversity metrics and their shortcomings for studying microbotanical remains, which are often morphologically redundant for identification. We developed Minimum Botanical Units as a new way of estimating how many plant types or parts are present in a microbotanical sample. In contrast to some previous work, we found no evidence that plant use is confined to the southern-most areas of Neanderthal distribution. Although interpreting the ecogeographic variation is limited by the incomplete preservation of dietary microremains, it is clear that plant exploitation was a widespread and deeply rooted Neanderthal subsistence strategy, even if they were predominately game hunters. Given the limited dietary variation across Neanderthal range in time and space in both plant and animal food exploitation, we argue that vegetal consumption was a feature of a generally static dietary niche.

Introduction

Neanderthals occupied environments drastically different from those where hominins first evolved. The ability of this hominin species to settle in diverse habitats, from the Mediterranean margin to steppic areas as cold as present-day Arctic tundra, implies that Neanderthals were successful at adapting to varied environments. In particular, their diets must have been flexible enough to allow them to thrive in these varied environments. However, some researchers have linked the disappearance of Neanderthals at the end of Middle Paleolithic to diets which were, relative to those of Upper Paleolithic peoples, narrower (Richards et al., 2001; Hockett and Haws, 2003,

2009; O'Connell, 2006). This idea is supported by stable isotopic and fauna data (Stiner, 1999; Richards et al., 2001; Conard et al., 2011). In this view, Neanderthal subsistence was reliant on a more restricted range of staples than that of modern humans, giving them a competitive disadvantage against Upper Paleolithic peoples.

Dietary breadth models, borrowed from the framework of behavioral ecology, have provided a means to interpret Paleolithic dietary adaptations. These models are predicated on the idea that foragers will select the foods that provide the most nutritional benefit (in calories or macro- or micronutrients) at the lowest costs, taking into account food processing requirements, within the constraints imposed by the environment (Winterhalder and Smith, 2000; Rothman et al., 2006). When the return rates for preferred foods decrease, due to climate change or population related hunting pressure, then more food types are added to the diet. A broadening diet is therefore not an adoption of an improved diet. It is just one of a number of possible responses to food scarcity that also includes intensity of food processing and technological adaptation.

Neanderthals are often interpreted as narrow spectrum foragers (Kuhn and Stiner, 2006; O'Connell, 2006; Stiner and Kuhn, 2009; Stiner, 2013). Models of Middle Paleolithic dietary ecology suggest that they hunted predominantly medium and large prime-age fauna with only infrequent use of small mammals, and aquatic and plant foods. Nitrogen stable isotope ratios indicate that they were at the top of the terrestrial food web and obtained most of their protein from medium and large-sized herbivores (Richards et al., 2000; Lee-Thorp and Sponheimer, 2006; Richards and Trinkaus, 2009; Wißing et al., 2015). Some zooarchaeologists have argued that this diet was stable over time, with little evidence of a chronological trend towards more diverse resource use (Stiner et al., 2000; Stiner, 2013). Surviving tool repertoires show scant evidence for the investment in specialized technology for collecting plants, fish, and small mammals (Kuhn and Stiner, 2006; O'Connell, 2006; Henry et al., 2014). A low diversification in food choice and high consumption of large and medium-sized game matches evidence from site density and their genetic history that imply sparse, dispersed populations of Neanderthals that did not deplete high-ranked prey items (Stiner, 1999; Stiner and Munro, 2002; Macdonald et al., 2009; Verpoorte, 2009; Castellano et al., 2014).

This view of rigid Neanderthal diets is complicated by recent studies suggesting evidence for variation in their diets. Prey selected by Neanderthals varies

throughout their range, often along ecological gradients. In southern regions, there is evidence for the consumption of low-ranked small game (Stiner 1994; Blasco and Fernández Peris 2009; Stiner and Kuhn 2009; Hardy et al. 2013; Salazar-García et al. 2013; Fiorenza 2015). In southern Iberia and western Italy, there is also zooarchaeological evidence of a contribution of marine resources (Stiner, 1994; Stringer et al., 2008; Zilhão et al., 2010). A preponderance of small game, including shellfish and tortoise (*Testudo* spp.), is also known from sites such as Kalamakia in Greece, Grotta dei Moscerini in Italy, Bajondillo Cave and Bolomor Cave in Spain and Nahal Meged in Israel (Stiner, 1994; Cortés-Sánchez et al., 2011; Blasco and Fernández Peris, 2012; Harvati et al., 2013). A study of tortoise remains at Nahal Meged showed a decrease in size due to hunting pressure and climate, beginning in the late Middle Paleolithic, suggesting that Neanderthals were collecting these foods at significant enough rates to reduce their body size (Stiner et al., 2000). In Cova del Bolomor, tortoises, rabbits and birds appear to have been frequently foraged during MIS 6 (Blasco and Fernández Peris, 2009; Salazar-García et al., 2013). In the warm MIS 5e interglacial, a greater proportion of small game is observed at several northern European sites despite the apparent continued dependence on large game (Gaudzinski-Windheuser and Roebroeks, 2011).

The current debate between a rigid, narrow diet and a more variable range of diets continues because most of our dietary evidence is fragmentary. As described above, the archaeological evidence is variable, and other potential sources of information, such as ethnographic studies, offer limited information. Recent foragers in northern environments provide a poor reference for Pleistocene foragers, in part because the treeless biomes of the Pleistocene have no analogue in the modern era (Stewart, 2005). The biomass of Pleistocene grasslands far exceeded that of present day Eurasian tundra, providing a greater number of available animals for Neanderthals. We know less about the productivity of plant foods in this ecological zone (Verpoorte, 2009), but energy-rich plants were available on the steppe-tundra and throughout western Eurasia (Sandgathe and Hayden 2003; Hardy 2010).

Relatively little evidence of plant use is available. Most isotopic profiles conducted so far have been produced from collagen, and thus reveal little information on the consumed macronutrients other than proteins that could have been obtained from vegetable resources. Macrobotanical remains that survive in a small number of archaeological sites—e.g., Kebara Cave (Lev et al., 2005) and

Douara Cave (Matsutani, 1987) in the Levant, and Gorham's and Vanguard Cave in Gibraltar (Barton et al., 1999; Gale and Carruthers, 2000)—suggest some level of plant use. The most comprehensive studies of dietary variability that incorporate plant foods stem from indirect evidence, such as dental microwear analyses, which have revealed that Neanderthals predominantly consumed meat, with a possible increased use of plants in the southern wooded parts of their range (El Zaatari et al., 2011; Fiorenza et al., 2011). The microwear of Neanderthals who inhabited cold-steppe environments resembled that of historic Fuegians who inhabited cold wet scrublands (Grine, 1986; Fiorenza et al., 2011). However, dental wear is silent on the number and types of plants consumed, or if low-ranked foods were consumed, meaning these studies create an incomplete picture of diet in different environments.

Neanderthals appear to have had more diverse diets in southern regions, possibly due to ecological variation (Stiner, 1999, 2001). Some researchers have pointed to legume assemblages from Kebara Cave (63–45 ka) and grass seed phytoliths from Amud Cave (70–55 ka), arguing that the use of more diverse resources was present already in the Middle Paleolithic (Madella et al., 2002; Lev et al., 2005). Others have studied starch and phytolith microremains trapped in dental calculus, and found that Neanderthal dental calculus from sites such as Spy and Shanidar indicate the use of date palm fruits and grass seeds in the Levant, and water lily tubers in northern Europe (Henry et al., 2011). In addition, geneticists have explored dental calculus aDNA as a source of dietary information, although plant DNA was found, its sheer rarity makes its significance hard to clarity (Weyrich et al., 2017). Despite these insights into Neanderthal use of plants, these samples are too widespread in time and space to give reasonable coverage of potential variation in Neanderthal diets. Importantly, these studies tell us little about the longevity of the Middle Paleolithic dietary niche. It is unknown if Neanderthal exploitation of plant foods broadened over the hundreds of thousands of years they occupied Eurasia in response to higher populations or milder climates, similarly to what is observed for the Upper Paleolithic and recent hunter-gatherers, or if variation is only linked to different environments.

To explore the flexibility of Middle Paleolithic dietary patterns through environmental variation, we investigated plant consumption as recorded in dental calculus from environments with varied vegetation and differing seasonal temperatures (given as mean winter and summer temperatures). We analyzed plant

microremains trapped in dental calculus from Neanderthal teeth from five archaeological sites: Vindija (Croatia), Grotta Guattari (Italy), Grotta Fossellone (Italy), Sima de las Palomas del Cabezo Gordo (Spain) and Kalamakia (Greece). These samples derive from a variety of regions and biomes across Europe: the northern Balkans, and the western, central and eastern Mediterranean (Fig. 1). We then identified microremains to examine the variety of consumed taxa. We predicted that if Neanderthal diet was flexible, the number of plant types represented in the calculus should be greater in warmer, more arboreal environments. It is well established that foragers living in warmer climates and lower latitudes acquire a greater proportion of food from plants (Kelly, 1995). Some researchers have found that increased reliance on plant foods also indicates the consumption of a larger number of different plant taxa (Marean, 1997), but we found no global surveys to confirm this idea. To overcome this, we collected the number of species recorded as food plants from seven foraging populations from a variety of environments and charted the relationship between climate and the number of plants used. Once complete, we explored if Middle Paleolithic dietary breadth varied in different climatic and ecological conditions. We predicted that if Neanderthal diet was flexible, the number of plant types represented in the calculus should be greater in samples from warmer, more arboreal environments.

Materials and methods

Sites and samples

We collected 28 samples of dental calculus from Neanderthal teeth representing no more than 22 individuals from five sites (Table 1). The sites range between 35 and 90 ka and represent a variety of habitats (Table 2). They range from open temperate environment at Vindija to Mediterranean mosaic woodland at Sima de las Palomas del Cabezo Gordo, and from cooler at Vindija to warmer at Kalamakia. This range reflects the bulk of environments Neanderthals occupied. Full site descriptions are provided in the Supplementary Online Material (SOM). From each site, we collected a variety of control samples, including sediments from the sites, dust on the skeletal material, and samples of the material in which the remains were stored (SOM Table S1). We also tried to sample dental calculus from the teeth of herbivorous and carnivorous fauna as an additional control and to explore if Neanderthals, like carnivores, consumed the stomach contents of herbivores (Buck

and Stringer, 2014). Unfortunately, we were able to access faunal material from only Vindija, Kalamakia and Sima de las Palomas del Cabezo Gordo. These samples included wolf (*Canis lupus*), which is mostly carnivorous but also known to consume some plant material; an indeterminate felid (cf. *Panthera*), cave bear (*Ursus spelaeus*), wild boar (*Sus scrofa*), an indeterminate micromammal, and deer (*Dama* and *Cervus).* These samples represent a range in dietary niches, from the purely carnivorous felid (Bocherens et al., 2011), through the wolf and bear that included increasing proportions of plant foods (Pacher and Stuart, 2009), to the purely herbivorous deer. In addition to the 28 Neanderthal calculus samples from the five sites that we processed for this study, we also included previously published data from a variety of other northern European, Levantine, and southern European sites (SOM S1; Salazar-García et al., 2013; Henry et al., 2014).

Dental calculus and control sampling

Neanderthal teeth from each site were examined for deposits of dental calculus situated on the tooth surface in a cleaned laboratory of the institution where each specimen is curated. Deposits of dental calculus were common on teeth examined, but it was not present on all specimens. We documented the dental calculus deposits with photography before sampling. We then collected 14 samples of dental calculus from the Vindija Neanderthal teeth (levels F, G1 and G3), five from the Grotta Guattari teeth (levels G0), two from the Grotta Fossellone teeth (level 4), seven from Sima de las Palomas del Cabezo Gordo teeth (Upper Cutting level 2 and I), and three from the Kalamakia teeth (Unit III and Lower IV; Table 1). Many of the sampled teeth had a visible band of hard supragingival dental calculus, except the Iberian teeth, which were encrusted in calcium carbonate. In these samples, when possible, we took ‘deep’ and ‘shallow’ samples. ’Shallow’ sediment samples were closer to the surface and likely to represent the sediment, while ’deep’ ones were more likely to include calculus. The ‘shallow’ samples were used as a control for contamination.

The sampling surface was gently dry brushed with a disposable toothbrush to dislodge contaminants at the sampling locations. We then used a dental scalar to remove small areas of dental calculus onto creased weighing paper underlain by aluminum foil. The material collected in the paper was then transferred to a microcentrifuge tube. After sampling, we photographed the teeth and the remaining

unsampled dental calculus. We then transported the samples to the Plant Foods laboratory at the Max Planck Institute for Evolutionary Anthropology (MPI-EVA).

To minimize risk of contamination from airborne modern plant material and laboratory supplies (Langejans, 2011; Crowther et al., 2014; Henry, 2014), we conducted a regime of weekly laboratory cleaning. All laboratory work surfaces were cleaned with hot water, washed with starch-free soap and with 5% sodium hydroxide (NaOH). To assess contamination types, we additionally performed wipe tests before and after weekly cleaning to quantify starch and other contaminants. Wipe tests retrieved settled particles of the surface area (74 x 43 cm^2) of the laboratory positive-pressure laminar flow hood used for mounting. Results of these intensive contamination control tests are found in the SOM Table S1.

Sample preparation and mounting

Using standard procedures (Power et al., 2014; Leonard et al., 2015), each sample was weighed and transferred to microcentrifuge tubes while in a clean laminar flow hood at the Plant Food Group Laboratories at the MPI-EVA. Each sample was then gently broken up with one second of micropestle use in a 1.5 ml Eppendorf microcentrifuge tube containing ~30 µl of a 25% glycerine solution to reduce sample loss due to static electricity. The samples were then centrifuged at 1691× g (Heraeus MEGAFUGE 16 with TX-400 fixed Rotors) for 10 minutes. These samples were mounted on glass slides and examined under brightfield and cross-polarized light on a Zeiss Axioscope microscope at 400× magnification. No decalcification treatment (HCl or EDTA) was used, in order to avoid additional processing steps that might remove or destroy microremains, particularly calcium oxalates. This leaves lumps of calculus but microremains still entrapped could be easily seen by adjusting focal plane. Identifying microremains embedded in situ was considered advantageous as it provided information on their origin. Studies on the effects of grinding on starches suggest that the gentle grinding used in this sample preparation method would have little impact on starches (Henry et al., 2009).

Identification and classification

We photographed and described recovered microremains using the international nomenclature codes (Madella et al., 2005; ICSN, 2011). Phytoliths were classified into conventional morphotypes, while we developed types to classify other

microremains based on shared morphology. Starches were classified into 23 types according to size, shape, the presence and prominence of lamellae, hilum morphology, formation characteristics (i.e., simple or compound), cross features, cracks and other surface features (SOM Table S2). Many of these types were considered redundant for identification purposes (e.g., types 17, 18 and 19; Table 3).

It is well known that some plants, such as Triticeae, produce starches with more than one distinct starch morphology; when this was documented, both morphologies were treated as one type (Peng et al., 1999). However, not all taxa are as well understood as Triticeae, and therefore it is possible for these less well-researched plants that several types may all have originated from a single taxon, or one type may be common to several taxa. Unlike starches, phytolith morphology has internationally classified codes and phytolith morphotype multiplicity is fairly well understood (Madella et al., 2005). For example, several phytolith types (short-cell, bulliform and psilate) may all represent a single species of grass. When possible, we identified the types to the most precise taxonomic level possible, usually family or genus (SOM S1 and Table S1). When possible, we scanned for potentially informative microremain damage such as phytolith weathering, partial starch gelatinization and other forms of heat damage (SOM Table S1). We found dry heat alteration to be a damage pattern diagnostic of starch contaminants from starch-free nitrile laboratory gloves.

Taphonomic biases

Different processes may affect the preservation of different microremain types unevenly. Both starch and phytolith preservation qualities vary according to species but methods have not yet been developed to control for this in dental calculus assemblages (Lu, 2000; Cabanes and Shahack-Gross, 2015; Power et al., 2015b). Food processing may also alter microremain content of plants. Different mastication patterns could potentially expose starch to varying levels of salivary amylase and influence starch survival. Cooking, (if widely practiced by Neanderthals) is expected to reduce starch content through gelatinization, but does not eliminate starch grains nor prevent them from entering dental calculus (Leonard et al., 2015). It is possible that starch could enter the mouth through the consumption of stomach contents (chyme). Given that many prey (ruminant and hindgut fermenter) can hydrolyze starch in their stomachs, we should not expect to see many starches entering human

dental calculus from the consumption of chyme, since most will have been already degraded (Owens et al., 1986). Phytoliths are often concentrated in the skin and husks of edible plants and food processing often reduces phytolith content of human food. However, herbivore chyme is probably rich in phytoliths, as phytoliths are preserved well in low pH environments (Madella and Lancelotti, 2012). An abundance of phytoliths and few starches in calculus may suggest consumption of stomach contents rather than direct consumption of plants.

Converting microremain diversity into measures of dietary breadth

Estimating dietary breadth from animal and plant remain assemblages is a major challenge in archaeological research (Grayson and Delpech, 1998). Until recently, there were no data on whether dental calculus could in any way reflect dietary breadth. Fortunately, recent experimental studies have shown that dental calculus assemblages can reflect a significant amount of dietary breadth and have laid a foundation on which to base expectations (Leonard et al., 2015; Power et al., 2015b).

Once we identified the microremains, we examined the total number of microremains per mg, but this was not ideal as it revealed little about diversity of types. Then we explored the number of microremain types and the Menhinick's index and Menhinick's index per mg of calculus. Menhinick's index is a richness metric common in ecological studies, and is the ratio of the number of taxa to the square root of sample size (Magurran, 2004). However, these metrics have major limitations as many starch and phytoliths types may be produced by the same plant. Furthermore, many starches and phytoliths are non-diagnostic, and among those that are diagnostic, they may indicate only broad categories such as dicot.

Therefore, to complement and refine this metric, we lumped all types that could be produced by one plant or plant part together. We call this standardized sum a minimum botanical unit (MBU; Table 3). MBUs may be individual plant taxa or plant parts. For example, a sedge cone phytolith, a chloridoid saddle phytolith and a Triticeae lenticular starch are three separate MBUs, while a Triticeae lenticular starch and a dendritic Long-Cell from Triticeae would be lumped together into one MBU (Table 3). The results of this novel approach were further standardized by combining it with a Menhinick's index by dividing the MBU by the square root of the total number of starch and phytoliths. Then with the MB-Menhinick's sums we

calculated other measures that may provide quantitative information about the assemblage. We also prepared ratios that are phytolith-specific for inferring phytolith producers, such as the monocot/dicot phytolith ratio, which may indicate contribution of grasses, sedges and other monocots versus the contribution of dicots; and the variable/consistent morphology (v/c) phytolith ratio, which indicates taxon (shown in SOM Table S2).

Climate and the number of consumed plant species in the ethnographic record

It is long established that the percent of diet derived from plants and terrestrial meat is strongly related to climate (Kelly, 1995), and it is expected that this applies to plant species used as well (Ichikawa and Terashima, 1996). Thus, we envisaged that there is a strong relationship between climate and the taxonomic breadth of plant food use in forager societies. Foragers in grassland environments are known to follow this pattern (Marean, 1997). A second major aspect of this study was examining the link between the dietary reliance on plant foods and the number of different types of plant taxa in a variety of environments, as it might be possible that ancient foragers might be highly reliant on plant foods but consume only a small number of taxa. The study aimed to provide verification that recent foragers, who rely on a greater amount of plant food, gather a greater range of plant species than foragers who use fewer plants. Due to the lack of non-grassland datasets on the number of plant species consumed by foragers, we tested if there is a relationship by plotting number of plant species documented as food items in ethnographic forager diets of the Labrador Inuit, Yupik, Aleutians, Ona, Ojibwa, Hadza, Alyawara, !Kung and Baka (Table 4; Fig. 2; Smith, 1932; Ager and Ager, 1980; O'Connell et al., 1983; Hattori, 2006; Veltre et al., 2006; Marlowe, 2010; Clark, 2012; Berihuete-Azorín, 2013; Crittenden and Schnorr, 2017). Although the data are sparse, the slope highlights that in warm climates, where plant foods are more important, foragers exploit a higher number of species. If Neanderthals behaved like modern humans, then we should also expect a climate-based variation in the number of plant species they consumed.

Paleotemperature and paleoenvironment reconstruction

To explore whether the number of plant foods in Neanderthal diets varied according to the habitat in which they lived, we needed detailed climatic

(temperature) and environmental (tree-cover) reconstructions of each of the investigated sites. For the climate, we used simulations for western Eurasia created as part of the Stage Three Project (van Andel and Davies, 2003). This project quantified climatic variables during much of the range of the last glaciation from 59 up to 24 ka, and generated four regional model simulations: MIS 3 warm climatic event, MIS 3 cold climatic event, the extremely cold Last Glacial Maximum (LGM), and finally a modern climatic model. These simulations may also be used to model conditions in other periods such as MIS 4, and are commonly used for this purpose (e.g., Aiello and Wheeler, 1995; Wales, 2012). Unfortunately, these models cannot account for third order climate fluctuations that occurred within these phases. However, when each simulation is examined with each Neanderthal site, we see that the variation in temperatures is driven more by the site's latitude and longitude than by the specific climatic period. Therefore, despite being relatively coarse-grained, these models allow us to quantify temperature variation. As more up-to-date simulations are available for the LGM, when predicting MIS 4 conditions, we used Community Climate System Model 4 (CCSM4) with 2.5 minutes resolution (Hijmans et al., 2005).

These simulations of temperature can be made more ecologically relevant by calculating effective temperature, a climatic predictor that evens out seasonal temperature variation. This powerful measure has been used to explain why recent forager subsistence varies latitudinally (Bailey, 1960; Binford, 2001). Effective temperature is based on three constants: the minimum mean temperature (18°C) that supports tropical plant communities (a 365 day growing season), the minimum temperature (10°C) at the start of the growing season at the zonal boundary of polar and boreal environments, and the minimum temperature (8°C) at the beginning of the growing season (Binford, 1980, 2001). Effective temperature (MET) is computed as follows:

$$ET = [(18 * MST) - (10 * MWT)] / (MST - MWT + 8)$$

where MST is mean temperature of the warmest month and MWT is mean temperature of the coldest month.

The Stage Three Project supplied mean temperature (ºC) 2 m above ground level. We matched plots of each simulation to the climatic phases in our sample set (Table 5), and we collected relevant values from each simulation plot and then calculated effective temperature for each hominin sample (Table 5).

To reconstruct the environment surrounding each site, we assessed tree cover using all published data on past habitats that existed at each site. We used investigations of macromammals, micromammals and pollen that record paleovegetation at different scales from local and regional studies to classify each environment. Based on the prevalence of tree cover, we assigned each sample as coming from open, mixed or closed habitats (Table 2). See each site paragraph in the SOM S1 for each designation.

Statistical analyses

To explore the relationships among environment, trends in foraging breadth, and microremains found in our samples and those from previous studies (SOM Table S3; Salazar-García et al., 2013; Henry et al., 2014), we fitted a random effect negative binomial model with likelihood ratio tests, using the glmer.nb function of the R package lme4 (Bates et al., 2013). We chose this negative binomial model because it is appropriate for count data that, like ours, is not normally distributed, and instead is skewed towards zero. We did not try to consider the potential effects of age at death or different age classes or sexes, as often this information is not available.

To calculate approximate sample size needed, we used Poisson regression power analysis in GPower 3.1 (Demidenko, 2007; Faul et al., 2009). The duration (defined as 'Mean exposure') 2.666 °C, as the dataset as a whole varies by 2.66°C with two tails, with a 'Base rate exp(β0)' that is estimated to be 5.75. Based on the results from the modern foragers (Fig. 2), we estimated a 12.6% increase in MBUs for every 1°C of effective temperature and we assigned a power of 0.85 at $\alpha = 0.05$. The resulting simulation revealed mean power values of 0.856 for a sample size of 42, although less than our sample size of 58 it is more than the number of samples from individual Neanderthals (37).

To proceed with the model, we collated multiple samples from each individual, and for which the recovered microremains were assigned to specific types. If any dental calculus samples produced no microremains, they were included as zero values. Our full model tested whether the number of MBUs was an effect of effective temperature, and the presence of tree cover at the site. We included the chronological age of the specimen as a control predicator. We prepared the data by z-transforming age and effective temperature. The site and analyst (R.C.P. and

A.G.H.) were treated as random intercept terms. To test the significance of the full model, it was compared with a null model excluding fixed effects of effective temperature, age of each fossil specimen, and tree cover. Variance inflation factors (VIF) were derived, to assess collinearity, from a standard linear model minus random effects and offsets. Variance inflation factors indicated that collinearity was not an issue (largest VIF = 1.26), but leverage suggests that potential influential cases exist. We tested model stability by excluding levels of the random effects (the random intercepts) one by one from the data set, running the full model and comparing the results with those from the original model that suggest no highly influential cases. To allow for the possibility of mixing between layers F, G1 and G3 in Vindija Cave, we built an identical model except that we recoded the samples from F and G1 as coming from G3. We performed similar procedures for removing overdispersion on this model (χ^2 = 42.574, df = 50, dispersion parameter = 0.851) and ensuring VIF was not an issue (largest VIF = 1.331).

Results

Contamination controls

Vindija Cave We collected some samples of faunal calculus, as well as adhesives used to hold Vindija tooth 11.39 (SOM Table S1). Microremains were found on the faunal calculus samples. These included small non-diagnostic starches on all three taxa (wolf, bear, and cat), and a number of phytoliths on wolf and bear (SOM Table S1). The number of microremain types is far lower than that seen in Neanderthal calculus samples. Of the microremains, some can be identified as not representing intentional diet (Triticeae on wolf), while others likely reflect dietary behavior, as they are consistent with the diets of these species (Pacher and Stuart, 2009). Present-day wolves consume plant matter, and plants may comprise up to 40% of their food intake in certain seasons (Meriggi et al., 1991). European wolves especially favor fruit, but wolves may also consume plants in stomach contents or intentionally consume grass to smooth digestion or ease parasite discomfort (Murie, 1944; Stahler et al., 2006).

Two control samples of mandible adhesive revealed 56 contaminant starches, but nearly all of these were highly diagnostic, heavily damaged potato starch. These starches are morphologically distinct from those in the Neanderthal dental calculus samples (SOM Table S1).

Grotta Guattari and Grotta Fossellone We took a variety of control samples, though not all preferred control types (e.g., faunal teeth) were available. Most controls were samples of adhesives used to bond bone, or washes of distilled water taken from the surfaces of the sampled mandibles. These contamination assays produced no or few microremains, and where microremains were found they showed a narrow range of types (Fig. 3; SOM Table S1). We found that these contaminating grains appeared distinct and usually occurred as starch aggregates, unlike more damaged and isolated starch in dental calculus samples (SOM Table S1). A Triticeae grass seed starch aggregate (type 20) was found in controls 2e and Fon3. None of this type of aggregate was found in the Neanderthal samples.

Sima de las Palomas del Cabezo Gordo In addition to controls (non-worked stone from archaeological strata, carnivore dental calculus, and packing cotton) published in Salazar-García et al. (2013), we sampled other packing material used to store hominin remains, as well as sediment found attached to hominin teeth. One sediment sample produced a single isolated subspherical starch. These results show a very low rate of background starch and phytoliths.

Kalamakia We took fauna control samples from the Kalamakia assemblage from wild boar, deer, and wild goat. These contamination controls exhibited low numbers of microremains, (Fig. 3; SOM Table S1). We found that these samples contained limited numbers of monocot and dicot phytoliths and plant tissue from grasses and dicots. All microremains are consistent with herbivore diets (SOM Table S1).

Dental calculus microremain assemblages and dietary breadth

Vindija Cave We collected calculus from six isolated teeth and five in situ teeth (catalogue numbers listed in Table 1). Isolated teeth comprised a right second molar, a lower second incisor, upper first incisor, upper canine, lower canine, and a lower second incisor. Our sample of in situ teeth comprised a lower canine, a lower third molar, an upper second molar, and a lower first molar. Microremains were recovered in all Neanderthal dental calculus samples, but there was major variation in the numbers and classes present. The plant microremain assemblages found on the Vindija samples is considerably more diverse than what was reported in the previous studies of Neanderthal calculus by having numerous non-starch and phytolith microremains (Hardy et al., 2012; Henry et al., 2012, 2014).

The highest numbers of microremains were found in Vindija dental calculus samples (SOM Table S1). Fifteen starches (type 15) displayed a lenticular cross-section, circular or subcircular plane view, a hilum exhibiting a thin line, and distinctive surface dimples and lamellae, clearly representing starches from Triticeae grass seeds (Fig. 4). They exhibited some damage and were isolated and clearly have a different origin than non-damaged Triticeae on the wolf sample (type 20). Although grass leaf microremains may arise from non-edible resources such as bedding, this seems unlikely to be the case for grass seeds.

Two of the starches (type 8) are likely to derive from a legume, based on their characteristics: circular, oval or ovoid shape, the presence of lamellae, and the characteristic longitudinal cleft fissure. We have observed these traits in peas (*Pisum* sp.), vetches (*Vicia* sp.), and vetchlings (*Lathyrus* sp.). Three other starches (Fig. 4; type 12 in SOM Table S2) displayed the size, highly faceted surface and polyhedral shape consistent with those of starches from hard endosperm not from Triticeae or legumes (Eliasson and Larsson, 1993). Plants that produce this starch morphology include nuts, hard seeds, seeds from grasses not in the Triticeae tribe, and seeds of sedges like *Schoenoplectus*. Two starches from underground storage organs (USOs) were evident from large elongated shape and highly eccentric polarization crosses. None of these legume, hard endosperm, or underground storage organ starches had specific enough morphological characteristics to classify them to a specific genus. The remaining starches fall into nine groupings, probably reflecting several taxa, but due to starch damage, redundant types and a limited reference collection, they cannot be identified. Five starch types also found in Neanderthal samples were also found in cave bear samples, but these were nondiagnostic types and thus do not necessarily represent the same taxa.

We recovered phytoliths from the Vindija dental calculus samples from dicot and monocots (SOM Table S1). Phytolith production between the two categories varies from 80:1 to 20:1 (Tsartsidou et al., 2007), while the ratios of monocot to dicot in our sample of Vindija Neanderthal dental calculus vary from 5:1 to 0.67:1, which suggests an abundance of dicot types such as fruits, nuts and leaves rather than grasses and sedges. Twenty-five spores were found, representing approximately five types of fungus. However, these are nondiagnostic and could represent mushroom-bearing higher fungi or lower fungi such as molds. Pollen was rare and only one Betulaceae pollen was found. Ten unsilicified plant tissue fragments were recovered,

two reflecting grass and one an unspecific monocot, but others were indeterminate. Phytoliths were classed into C3 Poaceae, Poaceae, monocot, dicot or dicot leaf, while starches were classified into Triticeae, legume, USO, non-Triticeae/ legume endosperm starch or a variety of unidentified types. Absolute minimum botanical units varied from 0 to 10 (Table 3; SOM Table S1).

Grotta Guattari and Grotta Fossellone We examined the calculus from the right lower third molar of Grotta Guattari II and the lower first molars (right and left), and a lower second incisor of Grotta Guattari III. Calculus samples from the five teeth from Grotta Guattari produced high numbers of microremains and microremain types. A total of 151 microremains were found in the dental calculus of the five teeth (SOM Table S1). Phytoliths and starches were classified into a similar, but lesser number of minimum botanical units as Vindija. Absolute minimum botanical units varied from 1 to 7 (Table 3; SOM Text S1).

Starch grains were found on four of the five teeth and totaled 69 grains. Six starches found still surrounded by cell walls were elongate ovoid in plane-view and oval in cross-section, with an eccentric polarization cross, all characteristics matching *Lilium* type starches (Fig. 4; SOM Table S1). One starch clearly represented a Triticeae grass seed starch. Further evidence of grass use is evident from intact grass leaf tissue found in one sample. The other detected starches represented five unknown types.

Thirty-nine phytoliths were recovered, 31 of which originated in monocot tissue and eight from dicot plants. Nine short cell rondel phytoliths were identified. One phytolith was a multicellular epidermal jigsaw morphotype, indicating dicot leafy or fruit matter. We also note the presence of a tracheid vessel, which is another dicot marker.

Other microremains were numerous. Ten spores were observed, some of which exhibited features that enabled us to identify them as coming from the bracken (*Pteridium* sp.). We also noted the presence of spores from *Nigrospora* sp. and fusiform spores, possibly indicative of boletoid fungi. Many bolete fungi are edible and widely consumed, while *Nigrospora* is a diverse genus of fungi that are mostly agents of decay. Five pollen grains were found including two Betulaceae pollens. In total 14 other cellular plant tissue fragments were noted, including vascular bundles, reflecting plants that entered the mouth. Also recovered were a number of stellate hairs and a pennate diatom.

We sampled dental calculus from the left lower first molar and second molar of Grotta Fossellone III. Eleven starches were found in the two Grotta Fossellone dental calculus samples. These comprised indeterminate starches that cannot yet be matched to reference material. Only one phytolith was found in the assemblage: a rondel phytolith from a grass. Additionally, one piece of monocot and one piece of unidentified plant tissue were found.

Sima de las Palomas del Cabezo Gordo For this study, we sampled dental calculus from six Sima de las Palomas del Cabezo Gordo teeth, including a lower third premolar, a lower canine, a lower third molar, a lower forth premolar, a upper incisor, a lower deciduous forth premolar, and a second molar, (catalogue numbers listed in Table 1). We found relatively few microremains in these samples, reflecting the very small amount of dental calculus in each sample. We recovered only five starches and phytoliths, and one diatom. None could be identified to plant taxon. The absolute minimum botanical units varied from 0 to 2 (Table 3; SOM Table S1).

Kalamakia We sampled dental calculus from three Kalamakia teeth: an upper third molar (KAL 3), an upper fourth premolar (KAL 5), and an upper second molar (KAL 8). Only a small number of starch grains and phytoliths were found on the three teeth. One phytolith was from a non-monocotyledon. Sixteen possible calcium oxalate forms were found. Calcium oxalate represents consumed plant matter, but it is readily soluble and occurs in most plants, and is therefore not assignable to taxon. Lastly, we found one fragmented sponge spicule. This last microremain likely entered the mouth through drinking water or in stomach contents. The absolute minimum botanical units varied from 1 to 10 (Table 3; SOM Table S1).

Dietary flexibility and dietary niche stability

As we showed earlier using the forager data survey, plant use among living groups is higher in warmer environments, where there is a higher number of taxa within the environment, so we should expect to see a similar pattern among Neanderthals. Using this observation, we predicted that if the breadth of Neanderthal plant use was driven by ecological conditions, then the number of consumed types should be influenced by effective temperature and tree cover. We produced a total MBU and a Menhinick's MBU index comparison of all available samples, including all previously published data and the new samples from this study. Although there is no distinct trend among Neanderthals from different periods or chronologies (Fig. 5;

SOM Table S4), there is a possible curvilinear relationship, with microremain numbers increasing with temperature until a peak is reached, at which point the numbers drop again. It is possible this pattern reflects the degradation of starches in the warmest environments (Langejans, 2010).

In our model to test if MBU is predicted by climate and environment, we found no relationship between the minimum botanical units found in calculus and the environmental conditions of the sample, even when accounting for the effects of variation between sites, analyst, age of remains (ka) and the number of microremains in a sample. More specifically, an increase in temperature did not lead to an increase in the number of plants represented in dental calculus and younger sites did not show an increase in the number of plants represented in dental calculus (χ^2 = 4.251, df = 3, p = 0.235; SOM Table S4). Even in the alternative model, which assumed bones in Vindija Cave layer G1 are older than thought and derive from G3, there was still no relationship (χ^2 = 4.335, df = 3, p = 0.227; SOM Table S4).

It is possible that we are not picking up on all of the variation in microremains because we were able to collect calculus from only one or two individuals at some sites. To test for sample size effects, we performed a resampling test, in which, for each population, we downsampled by choosing one individual randomly 1500 times (given that our smallest population was represented by one individual). This resampling provided a distribution of the average number of microremains for each population. In an ideal case, the distribution for each population would have been significantly different from the other populations (SOM Table S5). However, our pairwise tests failed to indicate differences in many of the pairwise comparisons of the population distribution.

Discussion

Microscopy revealed starch and phytoliths in most samples, but many samples were highly variable. However, the origin of much of the data's variability cannot be inferred, and could be due to the stochastic nature of the dental calculus dietary record or insufficient sample size. The variable results from calculus samples from the same individuals or even the same tooth support this (Vja-20, 21a and 21b). Due to this, the dental calculus record probably more accurately reflects group diet than individual diet. The development of a novel metric (minimum botanical unit) in this study has helped to overcome some of this variability. Minimum botanical units

proved to be a useful means to measure the lowest possible number of taxa represented. We found this metric could be used as a total or as part of a Menhinick's index.

Figure 3, SOM Fig. S1 and SOM Table S1 show that many dental calculus samples from Grotta Fossellone, Sima de las Palomas del Cabezo Gordo and Kalamakia yielded few microremains. Previous work that established baselines with chimpanzee (Power et al., 2015b) and living human (Leonard et al., 2015) populations indicates that this stochastic pattern is normal. These studies emphasize that we have not recovered information on the majority of consumed plants. These studies also indicate that, although plants are undoubtedly introduced to the oral cavity through non-dietary behaviors such as the inhalation or chewing of plants, these only comprise a modest component of microremain assemblages.

With these findings, we are able to show that Neanderthals in warmer environments who had better access to plant resources might not have necessarily used a far broader range of plant foods, and in some cases, they show less diversity than cool climate ones. However, we are cautious about these findings, as our ability to detect ecogeographical variation may be limited by the range of habitats included or sample size. Also, it is possible that plant remains such as starches are underrepresented in samples from warmer environments due to worse taphonomic conditions (Smith et al., 2001; Langejans, 2010). However, the phytoliths follow a similar pattern, despite being insensitive to temperature, suggesting that the pattern could be due to dietary, instead of taphonomic, trends. Our results on microremain diversity do not negate occlusal dental wear findings that link tree cover to plant use, as occlusal wear approximates only classes of the total diet and not its composition. Pleistocene plant foods likely reflect forest type (Mediterranean or Boreal) far more than tree cover alone. Open and mixed environments have less primary biomass than closed canopy environments, but they may offer significantly more edible plant biomass, as much of the biomass in forests consists of tree trunks, and is thus unavailable to hominin consumers (Odum, 1975). Pleistocene aridity may also have encouraged plant use; among recent foragers at a given latitude, plant consumption usually increased in more open environments, largely because aquatic animal foods are less available in these dryer habitats (Keeley, 1992).

The plants used indicate how Neanderthals sourced nutrition from their environment. We find evidence of the use of grass seeds, true lily tubers, legumes

and other starchy plants that leave no taxon-attributable types. Other microremain types included pollen and spores. Spores from Guattari III suggest interaction with fungi but these spores are too rare to ascertain the presence of deliberate use of fungi, such as the consumption of mushrooms (Power et al., 2015a). Not all recovered microremains reflect intentionally consumed food. Recovery of Betulaceae pollen and bracken spores may highlight use of birch or hazel and bracken, but, as these particles are excellent dispersers, they probably simply reflect characteristics of the suspensions and aerosols in the Pleistocene airborne environment. Other rare microremains, such as diatoms and sponge spicules, were probably introduced through drinking water or the consumption of animal stomach contents.

Some of the types that we were able to identify tell us about Neanderthal dietary behavior. In particular, many of the microremains come from foods that are often considered low-ranked, like grass seeds and tubers (Simms, 1985; Kelly, 1995). Grass seeds used at Vindija and at Grotte Guattari demonstrate an investment in a low-rank plant food in cool habitats of the northern Balkans and coastal Italy. The use of grass seeds is often linked to terminal Pleistocene Southwest Asian foragers, who invested in broad spectrum diets because grass seeds are usually costly to harvest and prepare for consumption (Simms, 1985). On the other hand, there is abundant evidence that groups like the Vindija Neanderthals were big game hunters and that energetic contribution from plants is not likely to have rivaled that of meat. Grass seeds are widely used by recent foragers in warm and cool environments (Lothrop, 1928; Simms, 1985; Harlan, 1989; Brand-Miller and Holt, 1998). Middle Paleolithic foragers probably only used grass seed as a limited component of the broader plant diet as this resource offers limited nutritional return (Simms, 1985). This is the pattern observed in Upper Paleolithic human foragers of Southwest Asia, where grass use is most prominent (Savard et al., 2006; Rosen, 2010).

It is unclear if Neanderthals gradually used a more diverse array of plants, alongside the modest increase in Neanderthal population from 70 ka onwards (Foley and Lahr, 2003; van Andel and Davies, 2003; Speth and Clark, 2006). If a chronological trend in vegetal dietary breadth is absent, it agrees with the lack of a trend in their predation niche before 55 ka. Although we cannot test if Neanderthal vegetal dietary breadth diverged from an overwhelmingly dominant hunting economy, they did use plant foods. While the exploitation of hard-to-catch game

714 necessitated a costly increase in technology, plants can often be harvested and
715 processed without the investment in technology. Although this may contradict
716 conventional expectations of glacial period foragers in Central Europe, the cold
717 temperatures of Pleistocene Eurasia may mislead us on the ecological productivity of
718 this region. The apparent patterns are better explained by decoupling seed and nut
719 use from the dietary expectations of the traditionally defined 'broad spectrum
720 revolution'. Seed and nut use may have been important foods throughout human
721 evolution (Hockett and Haws, 2003; Revedin et al., 2010; Crittenden and Schnorr,
722 2017). Additionally, taxonomic diversity in diet is just one way in which diet can
723 intensify due to demographic packing (population increase). Diet could intensify with
724 new hunting techniques and more elaborate processing, detoxification and cooking
725 (Wollstonecroft, 2011). Although an expanding plant food niche may be a sign of
726 demographic packing its presence need not signify a total investment in complex
727 foraging/broad spectrum foraging if such plant exploitation was possible without
728 costly plant harvesting and processing technology (Hockett and Haws, 2003). Non-
729 intensive use of these plants was possible with the technology available to
730 Neanderthals.

731 Neanderthals could have reduced their processing costs by making use of
732 caches of USOs and seeds, such as rodent stores, and by choosing to harvest the
733 plants during seasons when they were easiest to prepare. The raiding of rodent
734 stores requires little technology, though it often requires considerable ecological
735 knowledge (Jones, 2009). For example, Siberian peoples raided rodent stores to
736 obtain *Lilium* tubers all year round (Ståhlberg and Svanberg, 2010, 2012), but they
737 had to be able to discern edible tubers from toxic USOs. Neanderthals' ecological
738 knowledge may have also been useful for the consumption of grass seeds. As
739 Neanderthals exhibit no evidence of plant processing or food storage, we propose
740 that Neanderthals collected these seeds without laborious and expensive processing
741 costs. One of the few ways this is possible is by plucking green grain from spikelets
742 before they ripen and harden (Rosner, 2011). Unlike ripe grain, green grain requires
743 no grinding or pulverizing and may be consumed once dehusked, which can be done
744 by hand. Green grain starch granules are smaller than those of ripe grain, but they
745 share most morphological characteristics and are likely to be identified as coming
746 from grass seeds with our methodology (Evers, 1971). Green grain is a resource that
747 is available only in a narrow window before the grain ripens into a hard dry grain

(Rosner, 2011). This purported collection of green grain would be suggestive of precise seasonally-organized Neanderthal foraging. Unfortunately, there are insufficient data to reconstruct a seasonal round of plant food gathering, but gathering during the spring is evident.

Conclusions

The assemblages present evidence of Neanderthal use of plant as foods and complement our understanding of Neanderthal subsistence. This suggests that plant-harvesting strategies existed alongside their medium and large game hunting economy. Processing requirements of plant foods are often a limiting factor in their use (Kuhn and Stiner, 2006). Identifying the processes used to prepare or cook plant foods in different environments would likely reveal trends in how Neanderthals adapted to different diets and why they were replaced by Upper Paleolithic peoples. The ability of Neanderthals to anaerobically combust birch bark for tar manufacture hints that sophisticated heat-based food processing may have been available (Koller et al., 2001). Unfortunately, at this point we cannot survey food processing with our microbotanical dataset or the archaeological record as a whole.

Plant foods were likely valued for their micro- or macronutrient profiles rather than caloric energy alone. Hominin physiology limits the total dietary protein intake, impeding an absolute reliance on protein-rich foods such as terrestrial mammals (Cordain et al., 2000; Speth, 2010; Hockett, 2012). Recent foragers have avoided the effects of protein overconsumption by incorporating other macronutrients into their diet. Evidence from recent foragers worldwide suggests sourcing animal fat was a preeminent strategy for offsetting risk of protein poisoning (Speth and Spielmann, 1983; Cordain et al., 2000). However, obtaining concentrated sources of animal fat from a diet of terrestrial ungulates may not have always been possible. Triticeae, Fabaceae and Liliaceae offer rich sources of carbohydrates that may have offset the problems of lean protein consumption.

The incorporation of diverse plant foods, including those with low- or middle–ranking returns into the human diet, probably predates Neanderthal diets and has a long history in the human lineage, and it is likely that such diets persisted throughout hominin evolution mediated by energetic ecological necessity and labor availability. Similarly, resource depletion-driven subsistence change may have occurred at many points in hominin evolution in different food classes, as it is observed in present day

chimpanzees, where increases in chimpanzee populations have been linked to increased use of low ranked prey (Watts and Mitani, 2015).

Regarding Neanderthal subsistence, our model also finds no indication that plant use was confined to certain parts of their range; from the warm Mediterranean Basin to the cool habitats of Central Europe. Although microremains preservation may be biased, it is interesting that we did not find that a more diverse range of plants were consumed in southern areas. Although this may be a product of variability in the dental calculus dietary record, it could also reflect relatively unchanging strategies, stable thanks to their success. While past research has revealed unappreciated variability in Neanderthal animal food use (Stiner, 1994; Speth and Clark, 2006), as a whole, animal food provision centered on large to medium-sized game hunting and thus Neanderthals exhibit lower levels of diversity than early modern human counterparts in Eurasia (Richards et al., 2000, 2001). A large to medium-sized game hunting economy supplemented with plant foods may have evolved as a specialization strategy in response to Eurasian environments (Stiner, 2013). Synthesizing these patterns may imply that specialization was a defining force in Neanderthal ecology.

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References

Ager, T.A., Ager, L.P., 1980. Ethnobotany of the Eskimos of Nelson Island, Alaska. Arctic Anthropology 17, 26–48.

Aiello, L.C., Wheeler, P., 1995. The expensive-tissue hypothesis: the brain and the

digestive system in human and primate evolution. Current Anthropology 36, 199–221.

Bailey, H.P., 1960. A method of determining the warmth and temperateness of climate. Geografiska Annaler 42, 1–16.

Barton, R.N.E., Currant, A.P., Fernández-Jalvo, Y., Finlayson, J.C., Goldberg, P., MacPhail, R., Pettitt, P.B., Stringer, C.B., 1999. Gibraltar Neanderthals and results of recent excavations in Gorham's, Vanguard and Ibex Caves. Antiquity 73, 13–23.

Bates, D., Maechler, M., Bolker, B., 2013. lme4: Linear mixed-effects models using S4 classes. R package version 0.999999-2.999999.

Berihuete-Azorín, M., 2013. First archaeobotanical approach to plant use among Selknam hunter-gatherers (Tierra del Fuego, Argentina). Archaeological and Anthropological Sciences 5, 255–266.

Binford, L.R., 1980. Willow smoke and dogs' tails: Hunter-gatherer settlement systems and archaeological site formation. American Antiquity 45, 4–20.

Binford, L.R., 2001. Constructing Frames of Reference: An Analytical Method for Archaeological Theory Building Using Hunter-Gatherer and Environmental Data Sets. University of California Press, Berkeley.

Binford, L.R., Johnson, A.L., 2006. Program for calculating environmental and hunter-gatherer frames of reference (ENVCALC2). Java Version, August.

Blasco, R., Fernández Peris, J., 2009. Middle Pleistocene bird consumption at Level XI of Bolomor Cave (Valencia, Spain). Journal of Archaeological Science 36, 2213–2223.

Blasco, R., Fernández Peris, J., 2012. A uniquely broad spectrum diet during the Middle Pleistocene at Bolomor Cave (Valencia, Spain). Quaternary International 252, 16–31.

Bocherens, H., Drucker, D.G., Bonjean , D., Bridault, A., Conard, N.J., Cupillard, C., Germonpré, M., Höneisen, M., Münzel, S.C., Napierala, H., Patou-Mathis, M., Stephan, E., Uerpmann, H.-P., Ziegler, R., 2011. Isotopic evidence for dietary ecology of cave lion (*Panthera spelaea*) in North-Western Europe: Prey choice, competition and implications for extinction. Quaternary International 245, 249–261.

Brand-Miller, J.C., Holt, S.H., 1998. Australian aboriginal plant foods: a consideration of their nutritional composition and health implications. Nutrition Research

Reviews 11, 5–23.
Buck, L.T., Stringer, C.B., 2014. Having the stomach for it: a contribution to Neanderthal diets? Quaternary Science Reviews 96, 161–167.
Cabanes, D., Shahack-Gross, R., 2015. Understanding fossil phytolith preservation: The role of partial dissolution in paleoecology and archaeology. PLoS One 10, e0125532.
Castellano, S., Parra, G., Sánchez-Quinto, F.A., Racimo, F., Kuhlwilm, M., Kircher, M., Sawyer, S., Fu, Q., Heinze, A., Nickel, B., Dabney, J., Siebauer, M., White, L., Burbano, H.A., Renaud, G., Stenzel, U., Lalueza-Fox, C., de la Rasilla, M., Rosas, A., Rudan, P., Brajković, D., Kucan, Ž., Gušic, I., Shunkov, M. V., Derevianko, A.P., Viola, B., Meyer, M., Kelso, J., Andrés, A.M., Pääbo, S., 2014. Patterns of coding variation in the complete exomes of three Neandertals. Proceedings of the National Academy of Sciences of the United States of America 111, 6666–6671.
Clark, C., 2012. Inuit ethnobotany and ethnoecology in Nunavik and Nunatsiavut, northeastern Canada. Masters dissertation, Université de Montréal.
Conard, N.J., Kitagawa, K., Kro¨nneck, P., Bohme, M., Munzel, S.C., 2011. The importance of fish, fowl and small mammals in the Paleolithic diet of the Swabian Jura, Southwestern Germany. In: Clark, J.L., Speth, J.D. (Eds.), Zooarchaeology and Modern Human Origins: Human Hunting Behavior during the Later Pleistocene. Springer Science+Business, Dordrecht, pp. 173–190.
Cordain, L., Miller, J.B., Eaton, S.B., Mann, N., Holt, S.H., Speth, J.D., 2000. Plant-animal subsistence ratios and macronutrient energy estimations in worldwide hunter-gatherer diets. The American Journal of Clinical Nutrition. 71, 682–692.
Cortés-Sánchez, M., Morales-Muñiz, A., Simón-Vallejo, M.D., Lozano-Francisco, M.C., Vera-Peláez, J.L., Finlayson, C., Rodríguez-Vidal, J., Delgado-Huertas, A., Jiménez-Espejo, F.J., Martínez-Ruiz, F., Martínez-Aguirre, M.A., Pascual-Granged, A.J., Bergadà-Zapata, M.M., Gibaja-Bao, J.F., Riquelme-Cantal, J.A., López-Sáez, J.A., Rodrigo-Gámiz, M., Sakai, S., Sugisaki, S., Finlayson, G., Fa, D.A., Bicho, N.F., 2011. Earliest known use of marine resources by Neanderthals. PLoS One 6, e24026.
Crittenden, A.N., Schnorr, S.L., 2017. Current views on hunter-gatherer nutrition and the evolution of the human diet. American Journal of Physiscal Anthropology 163 S63, 84–109.

884 Crowther, A., Haslam, M., Oakden, N., Walde, D., Mercader, J., 2014. Documenting
885 contamination in ancient starch laboratories. Journal of Archaeological Science
886 49, 90–104.
887 Demidenko, E., 2007. Sample size determination for logistic regression revisited.
888 Statistics in Medicine 26, 3385–3397.
889 El Zaatari, S., Grine, F.E., Ungar, P.S., Hublin, J.-J., 2011. Ecogeographic variation
890 in Neandertal dietary habits: evidence from occlusal molar microwear texture
891 analysis. Journal of Human Evolution 61, 411–424.
892 Eliasson, A.C., Larsson, K., 1993. Cereals in Breadmaking: A Molecular Colloidal
893 Approach. CRC Press, New York.
894 Evers, A.D., 1971. Scanning electron microscopy of wheat starch. III. Granule
895 development in the endosperm. Starch - Stärke 5, 157–192.
896 Faul, F., Erdfelder, E., Buchner, A., Lang, A.-G., 2009. Statistical power analyses
897 using G*Power 3.1: Tests for correlation and regression analyses. Behavior
898 Research Methods 41, 1149–1160.
899 Fiorenza, L., 2015. Reconstructing diet and behaviour of Neanderthals from Central
900 Italy through dental macrowear analysis. Journal of Anthropological Sciences
901 93, 1–15.
902 Fiorenza, L., Benazzi, S., Tausch, J., Kullmer, O., Bromage, T.G., Schrenk, F., 2011.
903 Molar macrowear reveals Neanderthal eco-geographic dietary variation. PLoS
904 One 6, e14769.
905 Foley, R., Lahr, M.M., 2003. On stony ground: Lithic technology, human evolution,
906 and the emergence of culture. Evolutionary Anthropology 12, 109–122.
907 Gale, R., Carruthers, W., 2000. Charcoal and charred seed remains from Middle
908 Palaeolithic levels at Gorham's and Vanguard Caves. In: Stringer, C.B., Barton,
909 R.N.E., Finlayson, J.C. (Eds.), Neanderthals on the Edge. Oxbow Books,
910 Oxford, pp. 207–210.
911 Gaudzinski-Windheuser, S., Roebroeks, W., 2011. On Neanderthal subsistence in
912 last Interglacial forested environments in northern Europe. In: Conard, N.J.,
913 Richter, J. (Eds.), Neanderthal Lifeways, Subsistence and Technology: One
914 Hundred Fifty Years of Neanderthal Study. Springer Science & Business Media,
915 Dordrecht, pp. 61–71.
916 Grayson, D.K., Delpech, F., 1998. Changing diet breadth in the Early Upper
917 Palaeolithic of Southwestern France. Journal of Archaeological Science 25,

1119–1129.
Grine, F.E., 1986. Dental evidence for dietary differences in *Australopithecus* and *Paranthropus*: a quantitative analysis of permanent molar microwear. Journal of Human Evolution 15, 783–822.
Hardy, B.L., 2010. Climatic variability and plant food distribution in Pleistocene Europe: Implications for Neanderthal diet and subsistence. Quaternary Science Reviews 29, 662–679.
Hardy, B.L., Moncel, M.-H., Daujeard, C., Fernandes, P., Béarez, P., Desclaux, E., Chacon Navarro, M.G., Puaud, S., Gallotti, R., 2013. Impossible Neanderthals? Making string, throwing projectiles and catching small game during Marine Isotope Stage 4 (Abri du Maras, France). Quaternary Science Reviews 82, 23–40.
Hardy, K., Buckley, S., Collins, M.J., Estalrrich, A., Brothwell, D., Copeland, L., García-Tabernero, A., García-Vargas, S., de la Rasilla, M., Lalueza-Fox, C., Huguet, R., Bastir, M., Santamaría, D., Madella, M., Wilson, J., Cortés, A.F., Rosas, A., 2012. Neanderthal medics? Evidence for food, cooking, and medicinal plants entrapped in dental calculus. Naturwissenschaften 99, 617–626.
Harlan, J.R., 1989. Wild-grass seed harvesting in the Sahara and sub-Sahara of Africa. In: Harris, D.R., Hillman, G.C. (Eds.), Foraging and Farming: The Evolution of Plant Exploitation. Unwin Hyman, London, pp. 79–98.
Harvati, K., Darlas, A., Bailey, S.E., Rein, T.R., El Zaatari, S., Fiorenza, L., Kullmer, O., Psathi, E., 2013. New Neanderthal remains from Mani peninsula, Southern Greece: the Kalamakia Middle Paleolithic cave site. Journal of Human Evolution 64, 486–499.
Hattori, S., 2006. Utilization of Marantaceae plants by the Baka hunter-gatherers in southeastern Cameroon. African Study Monographs 33, 29–48.
Henry, A.G., 2014. Formation and taphonomic processes affecting starch grains. In: Marston, J.M., Guedes, J.D., Warinner, C. (Eds.), Current Methods in Paleoethnobotany. University of Colorado Press, Boulder, pp. 35–50.
Henry, A.G., Brooks, A.S., Piperno, D.R., 2011. Microfossils in calculus demonstrate consumption of plants and cooked foods in Neanderthal diets (Shanidar III, Iraq; Spy I and II, Belgium). Proceedings of the National Academy of Sciences of the United States of America 108, 486–491.

952 Henry, A.G., Hudson, H.F., Piperno, D.R., 2009. Changes in starch grain
953 morphologies from cooking. Journal of Archaeological Science 36, 915–922.
954 Henry, A.G., Ungar, P.S., Passey, B.H., Sponheimer, M., Rossouw, L., Bamford, M.,
955 Sandberg, P., de Ruiter, D.J., Berger, L., 2012. The diet of *Australopithecus*
956 *sediba*. Nature 487, 90–93.
957 Henry, A.G., Brooks, A.S., Piperno, D.R., 2014. Plant foods and the dietary ecology
958 of Neanderthals and early modern humans. Journal of Human Evolution 69, 44–
959 54.
960 Hijmans, R.J., Cameron, S.E., Parra, J.L., Jones, P.G., Jarvis, A., 2005. Very high
961 resolution interpolated climate surfaces for global land areas. International
962 Journal of Climatology 25, 1965–1978.
963 Hockett, B.S., 2012. The consequences of Middle Paleolithic diets on pregnant
964 Neanderthal women. Quaternary International 264, 78–82.
965 Hockett, B.S., Haws, J.A., 2003. Nutritional ecology and diachronic trends in
966 Paleolithic diet and health. Evolutionary Anthropology 12, 211–216.
967 Hockett, B.S., Haws, J.A., 2009. Continuity in animal resource diversity in the Late
968 Pleistocene human diet of Central Portugal. Before Farming 2009, 1–14.
969 Ichikawa, M., Terashima, H., 1996. Cultural diversity in the use of plants by Mbuti
970 hunter-gatherers in northeastern Zaire: an ethnobotanical approach. In: Kent, S.
971 (Ed.), Cultural Diversity among Twentieth-Centuary Foragers. Cambridge
972 University Press, Cambridge, pp. 276–293.
973 International Code for Starch Nomenclature (ICSN), 2011. The International Code for
974 Starch Nomenclature. http://fossilfarm.org/ICSN/Code.html (accessed 1 March
975 2015).
976 Jones, M., 2009. Moving North: Archaeobotanical evidence for plant diet in Middle
977 and Upper Paleolithic Europe. In: Hublin, J.-J., Richards, M.P. (Eds.), The
978 Evolution of Hominin Diets: Integrating Approaches to the Study of Palaeolithic
979 Subsistence. Springer, Dordrecht, pp. 171–180.
980 Keeley, L.H., 1992. The use of plant foods among hunter-gatherers : A cross-cultural
981 survey. In: Anderson, P.C. (Ed.), Prehistoire de l'Agriculture. Nouvelles
982 Approches Experimentales et Ethnographiques. National Center for Scientific
983 Research, Paris, pp. 29–38.
984 Kelly, R.L., 1995. The Foraging Spectrum: Diversity in Hunter-Gatherer Lifeways.
985 Eliot Werner Publications, New York.

Kirby, K.R., Gray, R.D., Greenhill, S.J., Jordan, F.M., Gomes-Ng, S., Bibiko, H.-J., Blasi, D.E., Botero, C.A., Bowern, C., Ember, C.R., Leehr, D., Low, B.S., McCarter, J., Divale, W., Gavin, M.C., Kirby, K.R., Gray, R.D., Greenhill, S.J., Jordan, F.M., Gomes-Ng, S., Bibiko, H.-J., Blasi, D.E., Botero, C.A., Bowern, C., Ember, C.R., Leehr, D., Low, B.S., McCarter, J., Divale, W., Gavin, M.C., 2016. D-PLACE: A global database of cultural, linguistic and environmental diversity. PLoS One 11, e0158391.

Koller, J., Baumer, U., Mania, D., 2001. High-Ttech in the middle Palaeolithic: Neandertal-manufactured pitch identified. Eurasian Journal of Archaeology 4, 385–397.

Kuhn, S.L., Stiner, M.C., 2006. What's a mother to do? The division of labor among Neandertals and modern humans in Eurasia. Current Anthropology 47, 953–981.

Langejans, G.H.J., 2010. Remains of the day-preservation of organic micro-residues on stone tools. Journal of Archaeological Science 37, 971–985.

Langejans, G.H.J., 2011. Discerning use-related micro-residues on tools: testing the multi-stranded approach for archaeological studies. Journal of Archaeological Science 38, 985–1000.

Lee-Thorp, J., Sponheimer, M., 2006. Contributions of biogeochemistry to understanding hominin dietary ecology. Yearbook of Physical Anthropology 43, 131–148.

Leonard, C., Vashro, L., O'Connell, J.F., Henry, A.G., 2015. Plant microremains in dental calculus as a record of plant consumption: a test with Twe forager-horticulturalists. Journal of Archaeological Science Reports 2, 449–457.

Lev, E., Kislev, M.E., Bar-Yosef, O., 2005. Mousterian vegetal food in Kebara Cave, Mt. Carmel. Journal of Archaeological Science 32, 475–484.

Lothrop, S.K., 1928. The Indians of Tierra del Fuego. Museum of the American Indian, New York.

Lu, T., 2000. The survival of starch residue in a subtropical environment. In: Wallis, D.M., Hart, L.A. (Eds.), Phytolith and Starch Research in the Australian-Pacific-Asian Regions: The State of the Art. Pandanus Books, Canberra, pp. 119–126.

Macdonald, K., Roebroeks, W., Verpoorte, A., 2009. An energetics perspective on the Neandertal record. In: Hublin, J.-J., Richards, M.P. (Eds.), The Evolution of

Hominin Diets: Integrating Approaches to the Study of Palaeolithic Subsistence. Springer, Dordrecht, pp. 211–220.
Madella, M., Alexandre, A., Ball, T., 2005. International code for phytolith nomenclature 1.0. Annals of Botany 96, 253–260.
Madella, M., Jones, M.K., Goldberg, P., Goren, Y., Hovers, E., 2002. The exploitation of plant resources by Neanderthals in Amud Cave (Israel): The evidence from phytolith studies. Journal of Archaeological Science 29, 703–719.
Madella, M., Lancelotti, C., 2012. Taphonomy and phytoliths: A user manual. Quaternary International 275, 76–83.
Magurran, A.E., 2004. Measuring Biological Diversity. Blackwell Publishing, Oxford.
Marean, C.W., 1997. Hunter–gatherer foraging strategies in tropical grasslands: model building and testing in the East African Middle and Later Stone Age. Journal of Anthropological Archaeology 16, 189–225.
Marlowe, F.W., 2010. The Hadza: Hunter-Gatherers of Tanzania. University of California Press, London.
Matsutani, A., 1987. Plant remains from the 1984 excavations at Douara Cave. In: Akazawa, T., Sakaguchi, Y. (Eds.), Paleolithic Site of Douara Cave and Paleogeography of Palmyra Basin in Syria: Part IV: 1984 Excavations. The University of Tokyo Press, Tokyo, pp. 117-122.
Meriggi, A., Rosa, P., Brangi, A., Matteucci, C., 1991. Habitat use and diet of the wolf in northern Italy. Acta Theriologica 36, 141–151.
Murie, A., 1944. The Wolves of Mount McKinley. Fauna of the National Parks of the United States. Fauna Series; no. 5. U.S. Government Printing Office, Washington.
O'Connell, J.F., 2006. How did modern humans displace Neanderthals? Insights from hunter-gatherer ethnography and archaeology. In: Conard, N.J. (Ed.), When Neanderthals and Modern Humans Met. Kerns Verlag, Tübingen, pp. 43–64.
O'Connell, J.F., Latz, P.K., Barnett, P., 1983. Traditional and modern plant use among the Alyawara of central Australia. Economic Botany 37, 80–109.
Odum, E.P. (Ed.), 1975. Ecology, 2nd Edition. Holt, Rinehart and Winston, New York.
Owens, F.N., Zinn, R.A., Kim, Y.K., 1986. Limits to starch digestion in the ruminant small intestine. Journal of Animal Science 63, 1634-1648.

Pacher, M., Stuart, A.J., 2009. Extinction chronology and palaeobiology of the cave bear (*Ursus spelaeus*). Boreas 38, 189–206.

Peng, M., Gao, M., Abdel-Aal, E.S.M., Hucl, P., Chibbar, R.N., 1999. Separation and characterization of A- and B-type starch granules in wheat endosperm. Cereal Chemistry 76, 375–379.

Power, R.C., Salazar-García, D.C., Wittig, R.M., Henry, A.G., 2014. Assessing use and suitability of scanning electron microscopy in the analysis of micro remains in dental calculus. Journal of Archaeological Science 49, 160–169.

Power, R.C., Salazar-García, D.C., Straus, L.G., González Morales, M.R., Henry, A.G., 2015a. Microremains from El Mirón Cave human dental calculus suggest a mixed plant-animal subsistence economy during the Magdalenian in Northern Iberia. Journal of Archaeological Science 60, 39–46.

Power, R.C., Salazar-García, D.C., Wittig, R.M., Freiberg, M., Henry, A.G., 2015b. Dental calculus evidence of Taï Forest chimpanzee plant consumption and life history transitions. Scientific Reports 5, 15161.

Revedin, A., Aranguren, B., Becattini, R., Longo, L., Marconi, E., Lippi, M.M., Skakun, N., Sinitsyn, A., Spiridonova, E., Svoboda, J., 2010. Thirty thousand-year-old evidence of plant food processing. Proceedings of the National Academy of Sciences of the United States of America 107, 18815–18819.Richards, M.P., Trinkaus, E., 2009. Out of Africa: modern human origins special feature: isotopic evidence for the diets of European Neanderthals and early modern humans. Proceedings of the National Academy of Sciences 106, 16034–16039.

Richards, M.P., Pettitt, P.B., Trinkaus, E., Smith, F.H., Paunović, M., Karavanić, I., 2000. Neanderthal diet at Vindija and Neanderthal predation: the evidence from stable isotopes. Proceedings of the National Academy of Sciences 97, 7663–7666.Richards, M.P., Pettitt, P.B., Stiner, M.C., Trinkaus, E., 2001. Stable isotope evidence for increasing dietary breadth in the European mid-Upper Paleolithic. Proceedings of the National Academy of Sciences of the United States of America 98, 6528–6532.

Rosen, A., 2010. Natufian plant exploitation: Managing risk and stability in an environment of change. Eurasian Prehistory 7, 117–131.

Rosner, A., 2011. Roasting green wheat in Galilee. Gastronomica 11, 60–68.

Rothman, J.M., Van Soest, P.J., Pell, A.N., 2006. Decaying wood is a sodium source

for mountain gorillas. Biology Letters 2, 321–324.
Salazar-García, D.C., Power, R.C., Sanchis Serra, A., Villaverde, V., Walker, M.J., Henry, A.G., 2013. Neanderthal diets in central and southeastern Mediterranean Iberia. Quaternary International 318, 3–18.
Sandgathe, D.M., Hayden, B., 2003. Did Neanderthals eat inner bark? Antiquity 77, 709–718.
Savard, M., Nesbitt, M., Jones, M.K., 2006. The role of wild grasses in subsistence and sedentism: new evidence from the northern Fertile Crescent. World Archaeology 38, 179–196.
Simms, S.R., 1985. Acquisition cost and nutritional data on Great Basin resources. Journal of California and Great Basin Anthropology 7, 117–126.
Smith, C.I., Chamberlain, A.T., Riley, M.S., Cooper, A., Stringer, C.B., Collins, M.J., 2001. Neanderthal DNA: Not just old but old and cold? Nature 410, 771–772.
Smith, H.H., 1932. Ethnobotany of the Ojibwe Indians. Bulletin of The Public Museum of the City of Milwaukee 4, 327–525.
Speth, J.D., 2010. The Paleoanthropology and Archaeology of Big-Game Hunting: Protein, Fat, or Politics? Springer, New York.
Speth, J.D., Clark, J.L., 2006. Hunting and overhunting in the Levantine Late Middle Palaeolithic. Before Farming 3, 1–42.
Speth, J.D., Spielmann, K.A., 1983. Energy source, protein metabolism, and hunter-gatherer subsistence strategies. Journal of Anthropological Archaeology 2, 1–31.
Ståhlberg, S., Svanberg, I., 2010. Gathering food from rodent nests in Siberia. Journal of Ethnobiology 30, 184–202.
Ståhlberg, S., Svanberg, I., 2012. Gathering dog's tooth violet (*Erythronium sibiricum*) in Siberia. Journal de la Societé Finno-Ougrienne 91, 349–351.
Stahler, D.R., Smith, D.W., Guernsey, D.S., 2006. Foraging and feeding ecology of the gray wolf (*Canis lupus*): lessons from Yellowstone National Park, Wyoming, USA. The Journal of Nutrition 136, 1923S–1926S.
Stewart, J.R., 2005. The ecology and adaptation of Neanderthals during the non-analogue environment of Oxygen Isotope Stage 3. Quaternary International 137, 35–46.
Stiner, M.C., 1994. Honor Among Thieves: a Zooarchaeological Study of Neandertal Ecology. Princeton University Press, Princeton.

Stiner, M.C., 1999. Paleolithic population growth pulses evidenced by small animal exploitation. Science 283, 190–194.

Stiner, M.C., 2001. Thirty years on the “Broad Spectrum Revolution” and Paleolithic demography. Proceedings of the National Academy of Sciences of the United States of America 98, 6993–6996.

Stiner, M.C., 2013. An unshakable Middle Paleolithic? Trends versus conservatism in the predatory niche and their social ramifications. Current Anthropology 54, S288–S304.

Stiner, M.C., Kuhn, S.L., 2009. Paleolithic diet and the division of labor in Mediterranean Eurasia. In: Hublin, J.-J., Richards, M.P. (Eds.), The Evolution of Hominin Diets: Integrating Approaches to the Study of Palaeolithic Subsistence. Springer, Dordrecht, pp. 155–168.

Stiner, M.C., Munro, N.D., 2002. Approaches to prehistoric diet breadth, demography, and prey ranking systems in time and space. Journal of Archaeol ogical Method and Theory 9, 181–214.

Stiner, M.C., Munro, N.D., Surovell, T.A., 2000. The tortoise and the hare: small game use, the Broad Spectrum Revolution, and Paleolithic demography. Current Anthropology 41, 39–79.

Stringer, C.B., Finlayson, J.C., Barton, R.N.E., Fernández-Jalvo, Y., Cáceres, I., Sabin, R.C., Rhodes, E.J., Currant, A.P., Rodríguez-Vidal, J., Giles Pacheco, F., Riquelme-Cantal, J.A., 2008. Neanderthal exploitation of marine mammals in Gibraltar. Proceedings of the National Academy of Sciences of the United States of America 105, 14319–14324.

Tsartsidou, G., Lev-Yadun, S., Albert, R.M., Miller-Rosen, A., Efstratiou, N., Weiner, S., 2007. The phytolith archaeological record: strengths and weaknesses evaluated based on a quantitative modern reference collection from Greece. Journal of Archaeological Science 34, 1262–1275.

van Andel, T.H., Davies, W., 2003. Neanderthals and Modern Humans in the European Landscape During the Last Glaciation: Archaeological Results of the Stage 3 Project. McDonald Institute for Archaeological Research, Cambridge.

Veltre, D., Pendleton, C., Schively, S., Hay, J., 2006. Aleut Ethnobotany: An Annotated Bibliography. Institute for Circumpolar Health Studies, Anchorage.

Verpoorte, A., 2009. Limiting factors on early modern human dispersals: The human biogeography of late Pleniglacial Europe. Quaternary International 201, 77–85.

Wales, N., 2012. Modeling Neanderthal clothing using ethnographic analogues. Journal of Human Evolution 63, 781–95.

Watts, D.P., Mitani, J.C., 2015. Hunting and prey switching by chimpanzees (*Pan troglodytes schweinfurthii*) at Ngogo. International Journal of Primatology 36, 728–748.

Weyrich, L.S., Duchene, S., Soubrier, J., Arriola, L., Llamas, B., Breen, J., Morris, A.G., Alt, K.W., Caramelli, D., Dresely, V., Farrell, M., Farrer, A.G., Francken, M., Gully, N., Haak, W., Hardy, K., Harvati, K., Held, P., Holmes, E.C., Kaidonis, J., Lalueza-Fox, C., de la Rasilla, M., Rosas, A., Semal, P., Soltysiak, A., Townsend, G., Usai, D., Wahl, J., Huson, D.H., Dobney, K., Cooper, A., 2017. Neanderthal behaviour, diet, and disease inferred from ancient DNA in dental calculus. Nature 544, 357–361.

Winterhalder, B., Smith, E.A., 2000. Analyzing adaptive strategies: Human behavioral ecology at twenty-five. Evolutionary Anthropology 9, 51–72.

Wißing, C., Rougier, H., Crevecoeur, I., Germonpré, M., Naito, Y.I., Semal, P., Bocherens, H., 2015. Isotopic evidence for dietary ecology of late Neandertals in North-Western Europe. Quaternary International 411, 327–345.

Wollstonecroft, M.M., 2011. Investigating the role of food processing in human evolution: A niche construction approach. Archaeology and Anthropology Sciences 3, 141–150.

Zilhão, J., Angelucci, D.E., Badal-García, E., D'Errico, F., Daniel, F., Dayet, L., Douka, K., Higham, T.F.G., Martínez-Sánchez, M.J., Montes-Bernárdez, R., Murcia-Mascarós, S., Pérez-Sirvent, C., Roldán-García, C., Vanhaeren, M., Villaverde, V., Wood, R.E., Zapata, J., 2010. Symbolic use of marine shells and mineral pigments by Iberian Neandertals. Proceedings of the National Academy of Sciences of the United States of America 107, 1023–1028.

Figure legends

Figure 1. Map of western Eurasia with the studied sites indicated.

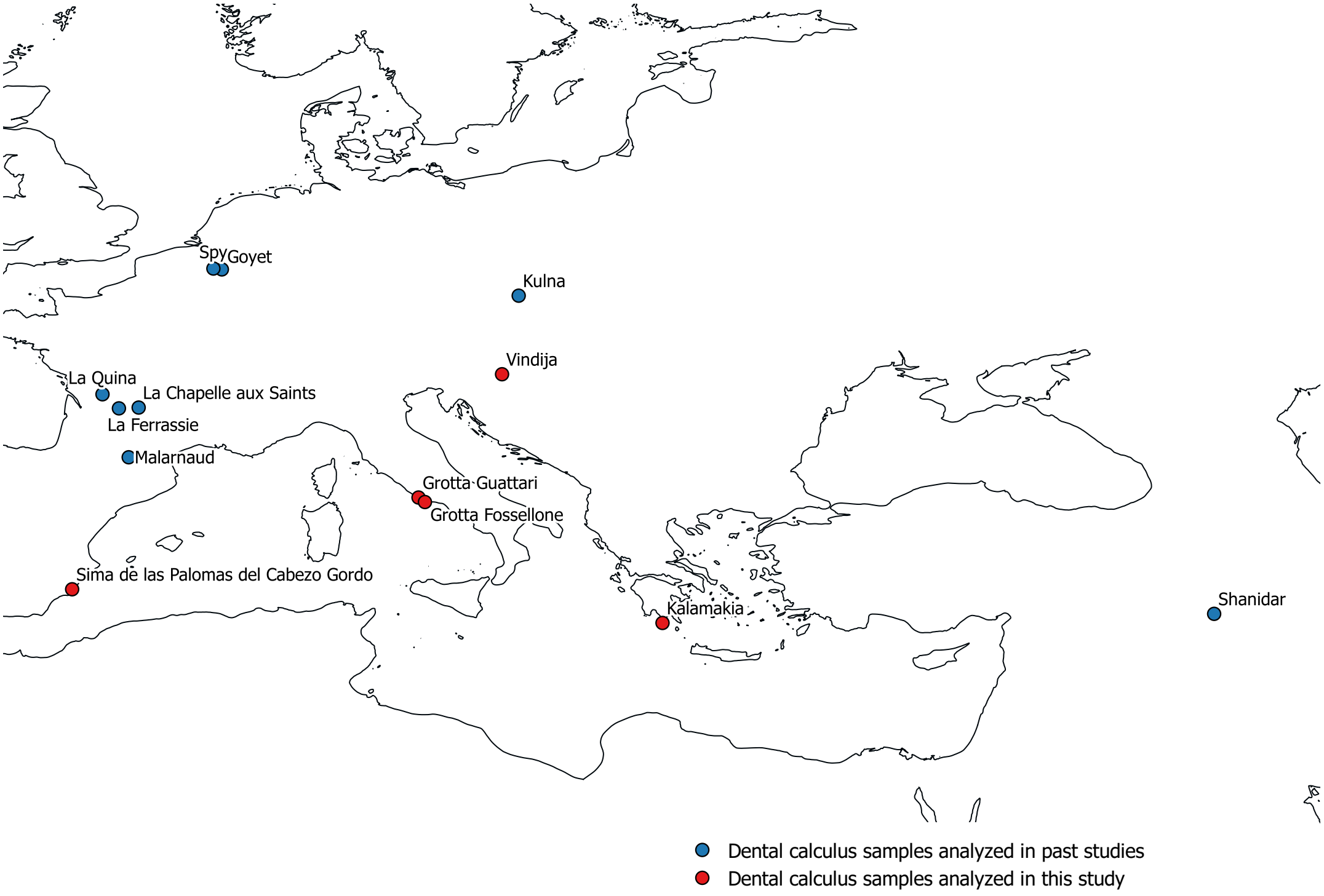
Figure 2. The relationship between warmer environments and effective temperature. Although only a limited amount of data are available, our survey includes samples

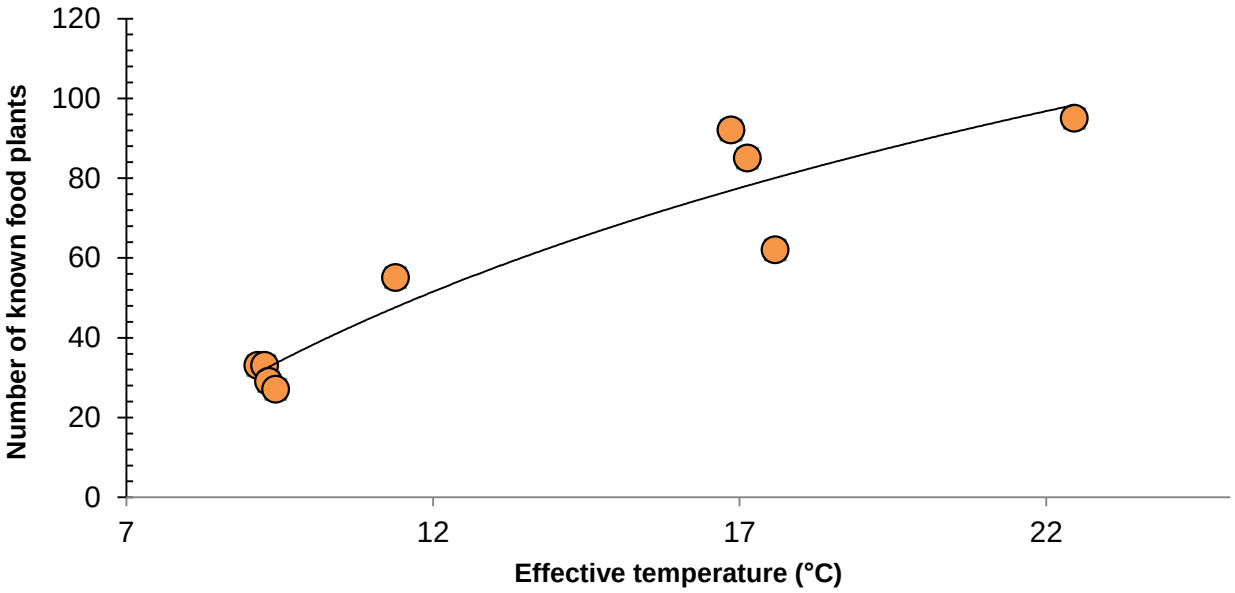
from polar, temperate, tropical and arid climates. Data available in Table 4. R^2 = 0.885.

Figure 3. The minimum botanical units of starch and phytoliths from Neanderthal calculus, fauna calculus and control sediments demonstrate that Neanderthal dental calculus samples show a distinct signal indicating they reflect hominin diet. Each circle represents an individual sample.

Figure 4. Mosaic of a small selection of microremains and comparative modern reference plant matter. Each scale bar represents 10 μm. Images give examples of microremain types and do not show identification criteria. For information on identification criteria and reference collection see SOM S1 (Table 3; SOM S1 Table S2). (a–b) Starch from Vindija Neanderthal identified as Triticeae under bright field and cross polarized light. (c–d) A reference Triticeae starch (*Triticum turgidum*.) under bright field and cross polarized light. (e–f) Plant matter with several ovoid starches resembling *Lilium* bulb starches under bright field (e) and (f) cross polarized light. (g–h) Reference bulb starches of *Lilium* sp. under bright field (g) and cross polarized light (h) in GTNIII. (i–j) Polyhedral starch under bright field (i) and cross polarized light (j). (k) Spore of *Pteridium* sp. (l) Diatom embedded in calculus. (m) Fragment of grass leaf. (n) Triporate Betulaceae pollen. (o) Unsilicified tracheid plant tissue.

Figure 5. A minimum botanical unit index of the starch and phytoliths from Neanderthal dental calculus shows that warmer climates are not associated with increased diversity. Samples are from Neanderthal remains presented in this study, as well as Salazar-Garcia et al. (2013) and Henry et al. (2014). Each dot represents an individual sample.


Spy
Goyet
Kulna
Vindija
La Quina
La Chapelle aux Saints
La Ferrassie
Malarnaud
Grotta Guattari
Grotta Fossellone
Sima de las Palomas del Cabezo Gordo
Kalamakia
Shanidar
Dental calculus samples analyzed in past studies
Dental calculus samples analyzed in this study


120
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Number of known food plants
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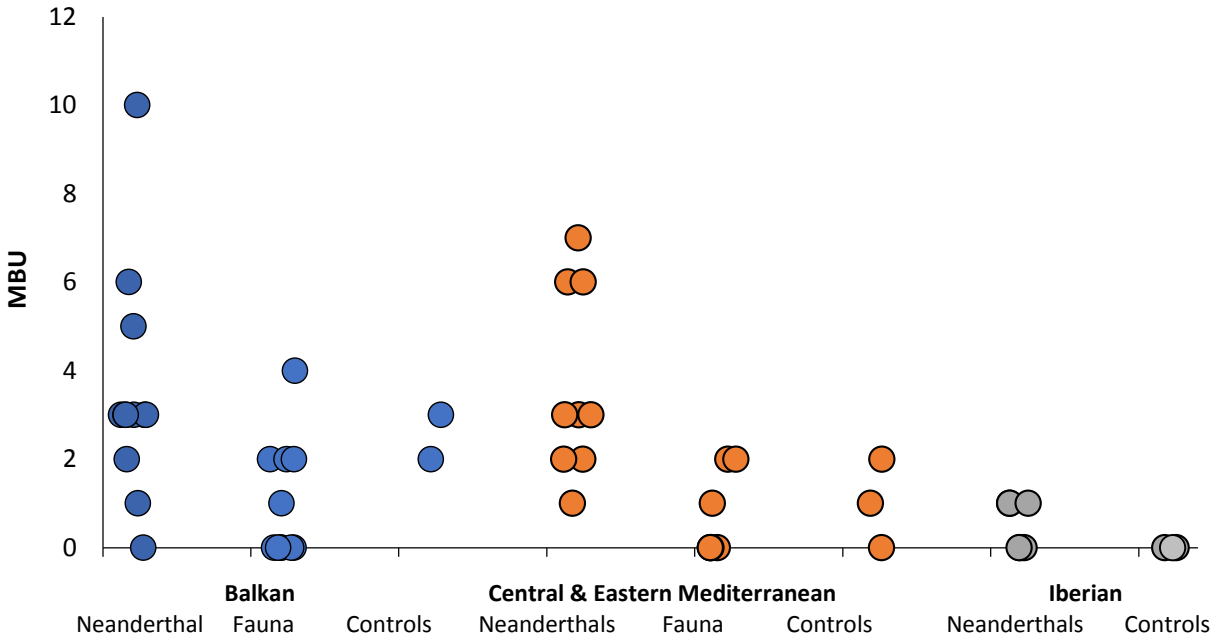
22
Effective temperature (°C)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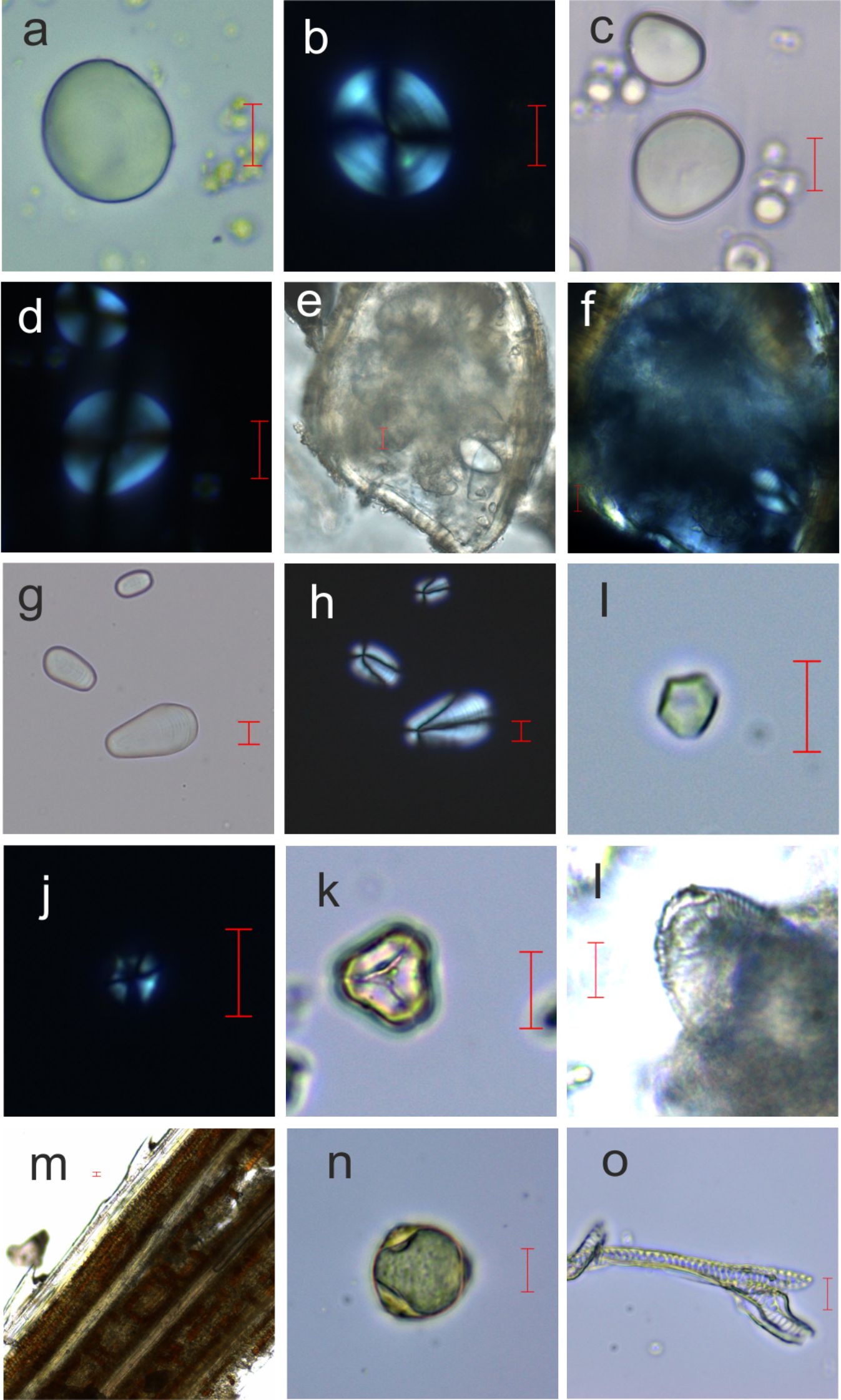
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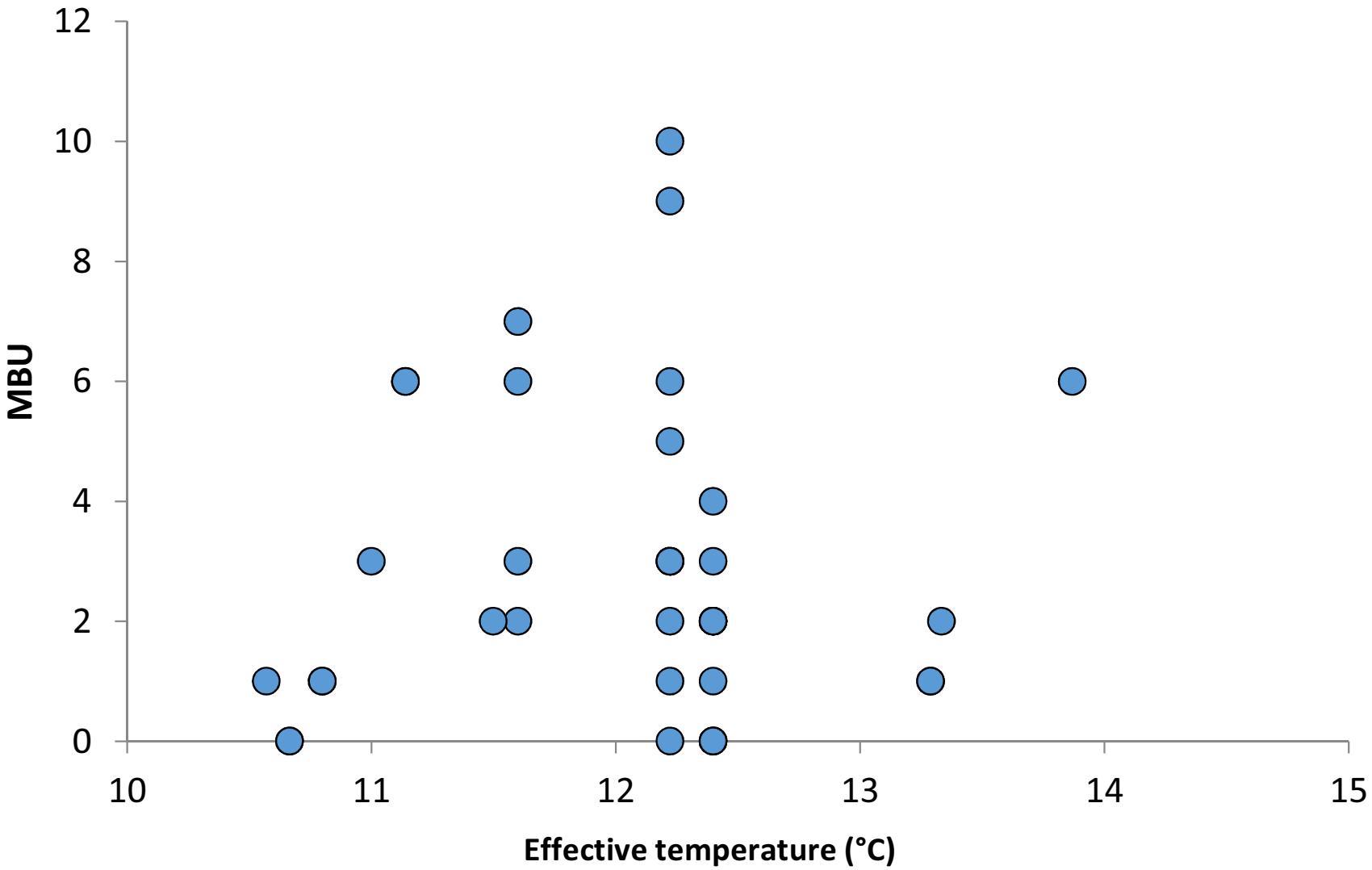
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Effective temperature (°C)

Table 1

Analyzed Neanderthal dental calculus from Vindija, Grotta Guattari, Grotta Fossellone, Sima de las Palomas del Cabezo Gordo and Kalamakia. Site ages are reported in Table 4. Multiple samples from the same individual are presented as a single entry.

Sample	Site	Specimen	Tooth	Weight (mg)
Vja-13	Vindija	12.1	R M^2	0.393
Vja-14	Vindija	12.2	R I_2	0.046
Vja-16	Vindija	12.4	R I^1	0.046
Vja-17	Vindija	12.5	R C^1	0.045
Vja-18	Vindija	12.6	L C_1	0.020
Vja-19	Vindija	12.7	L I_2	0.890
Vja-21	Vindija	11.39	R C_1, R M_1	0.502
Vja-23	Vindija	11.4	L M_1	0.377
Vja-24	Vindija	11.45	L M_3	0.672
Vja-26	Vindija	11.46	L M^2	0.865
FON1	Grotta Fossellone	Fossellone 3	L M_1	0.067
FON2	Grotta Fossellone	Fossellone 3	L M_2	0.100
GTN1	Grotta Guattari	Guattari II	R M_3	0.654
GTN2	Grotta Guattari	Guattari III	R M_1	0.871
GTN3	Grotta Guattari	Guattari III	L I_2	0.654
GTN4	Grotta Guattari	Guattari III	R I_2	0.258
GTN5	Grotta Guattari	Guattari III	L M_1	0.289
SP45	Sima de las Palomas del Cabezo Gordo	SP45	L P_3	0.080
SP54	Sima de las Palomas del Cabezo Gordo	SP54	R C_1	0.102
SP58a	Sima de las Palomas del Cabezo Gordo	SP58	R M_3	0.538
SP78a	Sima de las Palomas del Cabezo Gordo	SP78	L P_4	0.415
SP79	Sima de las Palomas del Cabezo Gordo	SP79	L I^1	—
SP83	Sima de las Palomas del Cabezo Gordo	SP83	R dP_4	0.090
SP84	Sima de las Palomas del Cabezo Gordo	SP84	M2	—
KAL_3	Kalamakia	KAL 3	L M^3	2.866
KAL_5	Kalamakia	KAL 5	L P^4	0.050
KAL_8	Kalamakia	KAL 8	R M^2	—

Table 2

Paleoenvironment reconstructions for each specimen used in this study.

Site	Specimen	Age (ka cal BP) [a]	Tree cover [b]	Paleotemperature [c]		ET [d]	Reference [e]
				December -February	June-August		
Vindija	12.1	34.3	open	-8	20	12.22	1
Vindija	12.2	34.3	open	-8	20	12.22	1
Vindija	12.4	34.3	open	-8	20	12.22	1
Vindija	12.5	34.3	open	-8	20	12.22	1
Vindija	12.6	34.3	open	-8	20	12.22	1
Vindija	12.7	34.3	open	-8	20	12.22	1
Vindija	11.39	45.5	open	-8	20	12.22	1
Vindija	11.45	45.5	open	-8	20	12.22	1
Vindija	11.46	45.5	open	-8	20	12.22	1
Vindija	11.4	45.5	open	-8	20	12.22	1
Grotta Guattari	Circeo 2	55	open	-4	16	11.71	1
Grotta Guattari	Circeo 3	67	open	-6	16	11.6	1
Grotta Fossellone	Fossellone 3	70	open	-6	16	11.6	1
Kalamakia	KAL 3	89.5	open	4	20	13.33	1
Kalamakia	KAL 5	62	open	5.9	18.45	13.29	1
Kalamakia	KAL 8	62	open	5.9	18.45	13.29	1
Sima de las Palomas	SP45	50	closed	4	20	13.33	1
Sima de las Palomas	SP50	50	closed	4	20	13.33	3
Sima de las Palomas	SP53	50	closed	4	20	13.33	3
Sima de las Palomas	SP54	50	closed	4	20	13.33	1
Sima de las Palomas	SP58	50	closed	4	20	13.33	1

Sima de las Palomas	SP60	50	closed	4	20	13.33	3
Sima de las Palomas	SP68	50	closed	4	20	13.33	3
Sima de las Palomas	SP74	50	closed	4	20	13.33	3
Sima de las Palomas	SP78	50	closed	4	20	13.33	1
Sima de las Palomas	SP79	50	closed	4	20	13.33	1
Sima de las Palomas	SP83	50	closed	4	20	13.33	1
Sima de las Palomas	SP84	50	closed	4	20	13.33	1
Sima de las Palomas	SP88	50	closed	4	20	13.33	3
Sima de las Palomas	SP100	50	closed	4	20	13.33	3
Kůlna	Kůlna 1	50	open	-8	16	11.5	2
Goyet	Goyet VII	40.5	open	-8	12	10.57	2
La Chapelle-aux-Saints	Chapelle 1	57	open	-4	12	10.67	2
Malarnaud	Malarnaud 1	75	mixed	0	12	10.8	2
La Ferrassie	LFI	39	closed	0	12	10.8	2
La Ferrassie	LFII	39	closed	0	12	10.8	2
La Quina	Quina V	64	mixed	-0.55	12.65	11	2
Spy	Spy 2	36.5	open	-6	14	11.14	2
Spy	Spy 2	36.5	open	-6	14	11.14	2
Spy	Spy 1	36.5	open	-6	14	11.14	2
Spy	Spy 1	36.5	open	-6	14	11.14	2
Shanidar	Shani III	48	closed	2	25	13.87	2
Shanidar	Shani III	48	closed	2	25	13.87	2

Shanidar	Shani III	48	closed	2	25	13.87	2	

[a] Site age is calculated by using the mean of the calendric ages.

[b] Tree cover is calculated with pollen and fauna data.

[c] Paleotemperature is calculated from the Stage Three Project dataset.

[d] ET= effective temperature (which is a measure of biologically relevant temperature).

[e] References: 1= this study; 2= Henry et al. (2014); 3 = Salazar-García et al. (2013).

18 **Table 3**

19 Counted microremains and their assigned minimum botanical unit.

20

Starches		Phytoliths	
Type	Minimum botanical unit	Type	Minimum botanical unit
Type 1	Type 1 starch	Long-Cell psilate	Poaceae
Type 2	Type 2 starch	L-C verrucate (non-generic type)	*Celtis*/ *Boehmaria*/ *Morus* or *Urtica*
Type 3	Starchy seed producer type 1	L-C wavy	Poaceae
Type 4	USO starch	L-C sinuous	C3 Poaceae
Type 5	Starchy seed producer type 2	Polylobate	C3 Poaceae
Type 6	Type 6 starch	Trichome	Poaceae
Type 8	Legume starch	Rondel	C3 Poaceae
Type 8	Type 8 starch	Bulliform fan	Poaceae
Type 9	Type 9 starch	Bulliform Parallelepipedal	Poaceae
Type 10	Type 10 starch	Monocot hair	Monocot
Type 11	Type 11 starch	Cylindroid	Conifer/dicot
Type 12	Type 12 starch	Dicot hair	Dicot
Type 13	Type 13 starch	Globular sinuate/ rugulate	Dicot
Type 14	Type 14 starch	Ellipsoid rugulate	Dicot
Type 15	Triticeae	Parallelepipedal	Dicot
Type 16	Type 16 starch. Hard endosperm starch.	Parallelepipedal thick	Dicot
Type 17	Redundant starch	Parallelepipedal elongate psilate	Dicot
Type 18	Redundant starch	Parallelepipedal thin rounded ends	Dicot
Type 19	Redundant starch	Multicellular Long-ells	Monocot

Type 21	Black bindweed (Cf. *Fallopia* sp.)	Multicellular polyhedrons	Dicot leaf
Type 22	Cf. *Lilium* sp.	Spheroid granulate	Non Poaceae
Type 23	Redundant starch	Mesophyll	Dicot leaf
Other	Redundant starch	Indet. Multicell	Plant
Partially gelatin., large ovoid	Redundant starch	Indet. Hair	Plant
Pos/Dmg	Redundant starch	Epidermal	Dicot leaf
		Plate	Dicot leaf/fruit
		Calcium oxalate	Plant

21

22

Table 4

Relationship between effective temperature and the number of taxa in the diet of recent foragers.

Group	Region	Effective temperature (°C)	Plant dependence (%) [a]	Number of food plants	Citation
Labrador Inuit	NE Canada	9.149	0.01	33	Clark, 2012
Aleutian	W Alaska	9.258	1	33	Veltre et al., 2006
Yupik	W Alaska	9.320	1	29	Ager and Ager, 1980
Ona	S Argentina and Chile	9.436	5	27	Berihuete-Azorín, 2013
Ojibwe [b]	Canada, United States border	11.395	11	55	Smith, 1932
Alyawara	Central Australia	16.867	65	92	O'Connell et al., 1983
!Kung	S Africa	17.131	67	85	Crittenden and Schnorr, 2017
Hadza	E Africa	17.586	60	62	Marlowe, 2010
Baka	Cameroon	22.463	85	95	Hattori, 2006

[a] Estimate of vegetal intake based on Binford forager dataset (Binford, 2001; Binford and Johnson, 2006; Kirby et al., 2016).

[b] Grouping averaged plant food and climate values from North Albany Ojibwa, Rainy River Ojibwa, Eastern Ojibwa, Round Lake Ojibwa and Wegamon Ojibwa.

33 **Table 5**

34 Stage 3 Project simulations used to predict average summer and winter

35 temperatures experienced by each Neanderthal (Wales, 2012).

Interval	Phase	Simulation model used	Age (ka cal BP)
MIS 5d	Early Glacial Stadial Phase	Warm	117–105
MIS 5c	Early Glacial interstadial Phase	Warm	105–95
MIS 5b	Early Glacial Stadial Phase	Warm	94–85
MIS 5a	Early Glacial Warm Phase	Warm	85–74
MIS 4	Transitional Phase	Warm	74–66
MIS 4	First Glacial Maximum	Last Glacial Maximum	66–59
MIS 3	Stable Warm Phase	Warm	59–44
MIS 3	Transitional Phase	Warm	44–37
MIS 3	Early Cold Phase	Cold	37–27

36

Supplementary Online Material (SOM)

Dental calculus indicates widespread plant use within the stable Neanderthal dietary niche

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SOM S1

Archaeological sites where samples were analyzed

We prepared data from past dental calculus studies for a comparative analysis (Salazar-García et al., 2013; Henry et al., 2014). This dataset included already published starch and phytolith counts from five other Middle Paleolithic sites as well more data from Sima de los Palomas. As other microremains are not included in previous published studies, we included only starch and phytoliths in our model. Our samples were weighed in mg, but weights for all eight sites are not available. Similarly, in the datasets presented in this paper we treated starches of the same type that occurred as lumps as one starch, as accurately counting each starch in a lump is not possible. We collected the updated estimated date range for each site and used the median value.

Vindija Cave This cave is situated on the southwest slopes of Kriznjak Peak in the Hrvatsko Zagorje region of northern Croatia (46.302238, 16.080102). Early exploration of the site began in 1928 with small-scale excavations. Malez and colleagues conducted large-scale archaeological excavations between 1974–1986 and 1993–1994. These uncovered a complex of 10 m deep strata of 16 layers, with abundant paleontological, archaeological and hominin material. A considerable number of hominin skeletal fragments were found in the cave deposits deriving from five or more individuals (Karavanić and Smith, 1998). A portion of this material was Mousterian-associated, and researchers identified the material as coming from Late Pleistocene Neanderthals due to its less pronounced archaic traits (Smith, et al., 1985). A radiocarbon date of >45.5 ka cal BP (Krings et al. 2000; see Table 4), and a U/Th date of a cave bear bone of 50.3 ka cal BP (Wild et al., 2001) have assigned layer G3 to MIS 3. Direct AMS ultrafiltration dating of hominin remains from layer G has not found uniformity, with dates ranging from 33,371 ± 399 to 35,382 ± 2224 ka cal BP to before 40,000 ka BP, (Higham et al., 2006; Devièse et al., 2017). Archaeologists found Neanderthal material mostly in layers G1 and G3, but also four teeth in Layer F (of which we sampled two: 12.2 and 12.6). There was also modern human material in Layer D (MNI < 10). G3 is unambiguously Mousterian, while layers G1 and F contain some Aurignacian lithic material. However, dating and morphological evidence has firmly established the presence of Neanderthals in these

layers, and cryoturbation is likely to have been responsible for bone displacement (Wolpoff et al., 1981; Higham et al., 2006; Frayer et al., 2010). Aurignacian lithic typology and early Upper Paleolithic bone points are known in layers F and G1. The relatively low density of Aurignacian lithics, the mixing evident from contradictory dates, and the evidence of Neanderthal traits on the teeth (Frayer et al., 2010) suggest that the layer F teeth are in fact Neanderthal remains from layer G, so we feel comfortable including them in our analyses. Excavators found red deer (*Cervus elaphus*), elk (*Alces alces*), giant deer (*Megaloceros giganteus*) and aurochs (*Bos primigenius*) in layer G3, chamois (*Rupicapra* sp.), roe deer (*Capreolus capreolus)* and Merck's rhinoceros (*Stephanorhinus* sp.) in layer G1 and bison (*Bison* sp.), ibex (*Capra* sp.) and Merck's rhinoceros in layer F. Micromammals such as bank voles (*Myodes glareolus*) were found in layer G (Mauch Lenardić, 2014). These taxa generally suggest continental conditions, and fauna such as roe deer and bank voles suggest at least a degree of tree cover, perhaps as parkland or riverine mosaics.

Grotta Guattari This site is one of a complex of caves located in Monte Circeo, a limestone massif in Lazio, Central Italy (41.228178, 13.079801). The site was discovered in 1939 inadvertently when surface fauna and the remains of one Neanderthal (Guattari I) in layer G0 were discovered. Later explorations found more Neanderthals, firstly in a bone scatter (Guattari II) in layer G0, and subsequently in breccia (Guattari III) at the cave entrance (Sergi, 1954). The cave has seven stratigraphic layers (G1-G7) and surface layer (G0) but G0 is not vertically discrete partially due to carnivore disturbance (Stiner and Kuhn, 1992). Layers G1–G5 produced lithic artefacts and were deposited rapidly, but layers G6–G7 are beach deposits that accumulated more slowly. Researchers identified the hominin remains as morphologically Neanderthal with a 'classic' morphotype, suggesting they date to the Late Pleistocene (Howell, 1957). Stratigraphically below the fossils are the sequence's basal marine-influenced deposits (G7), which are thought to relate to the final high sea level event of oxygen isotope stage 5a (84–74 ka; Martinson et al., 1987; Grün and Stringer, 1991). U-series and electron spin resonance dating of calcite encrustations on bones and mammal teeth from the stratum that produced Guattari I and II suggest a date of 60–50 ka, while Guattari III dates to the end of MIS 5, 74–60 ka (Grün and Stringer, 1991; Schwarcz and Schoeninger, 1991). Regional palynology studies indicate grasslands in cold periods and tree cover in warmer phases (van Andel and Tzedakis, 1996; Follieri et al., 1998). A variety of

fauna was found on site. Some fauna, such as ibex, indicate mountainous open habitats. Others, such as boar (*Sus scrofa*) and roe deer, are thought to indicate tree cover or shrub, while many other fauna, such as Merck's rhinoceros, aurochs and mammoth (*Elephas antiquus*), may represent either open grasslands or parkland or more mixed environments Extreme cold-adapted species like reindeer (*Cervus elaphus*) or arctic fox (*Vulpes lagopus*) are absent on coastal sites in the region, demonstrating the absence of a bitter cold environment (Kuhn, 1991).

Grotta Fossellone This site is also a cave in the Mount Circeo Complex at Lazio in Central Italy (41.25, 13.033333). Archaeologists excavated the cave deposits between 1937–1940 and 1947–1953 (Blanc, 1954), finding sediments 14 m thick, consisting of 51 levels. Blanc (1954) reported the presence of Upper Paleolithic Aurignacian and Middle Paleolithic Mousterian deposits. This sequence can be divided into three entities: the first and lowest group (levels 41–23) has a Mousterian industry, the second group (level 21) has a Middle Aurignacian deposit, and the third group (levels 19–1) is a deposit with only rare lithics and bone material (Vitagliano and Piperno, 1991). The remains of one Neanderthal (Fossellone 3) was found low in the sequence in 1954 (Mallegni, 1992). Radmilli (1962) described Mousterian level 4 as dating to the MIS 5a to MIS 4 (Late Würm I/Early Würm II). Mousterian associated fauna include cave hyena (*Crocuta spelaeus*), horse (*Equus caballus),* leopard (*Panthera* sp.), Merck's rhinoceros, red deer, indeterminate bovid, elephant (*Elephas* sp.) and ibex (Blanc, 1954).

Sima de las Palomas del Cabezo Gordo It is a 31 m-deep karstic cave overlooking the Mediterranean Sea, opening at 125 m above it (37.801103, -0.90646) in a hill of Permo-Triassic marble called Cabezo Gordo, in Murcia, SE Spain. Much fossiliferous breccia was extracted from the 18 m-deep entrance shaft by 19th-century miners and discarded as rubble. Inside the shaft there remained untouched a column of breccia in which a speleologist descending on an abseil rope in 1991 observed a fossil (SP1) of a Neanderthal mandible fused to the maxillae. In 1992, methodical field research commenced. Neanderthal skeletal elements, Late Pleistocene faunal remains, and Mousterian Middle Paleolithic artifacts were recovered by sieving brecciated rubble, and systematic excavation began of the uppermost (coarse, beige) sediment in the remaining breccia column in the shaft, from which similar finds were forthcoming (Walker et al., 2008; Trinkaus and Walker, 2017). This sediment, which also contained a deeply-lying, dark-gray lens of burnt

sediment, corresponds to Late Pleistocene infill (reaching up to a roof of rock overhanging the shaft) that accumulated against a partly-cemented tumble of massive scree (Conglomerate A, CA) with an unconsolidated sloping surface through which various small elements probably migrated into the later sediment, rapidly accumulating around it. Near-overlap of 95% confidence intervals exists for some age estimates on materials from CA, the later sediment around it, and the underlying Conglomerate B (CB). Chronological analysis is hampered by availability for excavation of an area confined to 5 m^2 at the rim of the miners' 18 m-deep yawning hole that restricts stratigraphical inspection to 3 vertical sections. Published age estimates (95% confidence intervals shown in brackets) are the following (Trinkaus and Walker, 2017): 56.0 + 13 ka, –10 (U-ser, M5 from CB); 54.1 ± 7.7 ka (61.6–46.6 ka; U-ser, APSLP1 on SP96 in CA); 51.0 ± 2.5 ka (53.5 – 48.5 ka; U-ser, APSLP6 beside CA in surrounding sediment); 43.8 ± 1.5 ka (45.3–42.3 ka; U-ser, APSLP4 in sediment accumulated around CA); 54.7 ± 4.7 ka (64–45 ka; OSL; X2509 from burnt lens in sediment accumulated around CA); 35.03 ± 0.27 ka (41–38.9 ka; ^{14}C, OxA-15423 on burnt lagomorph bone in burnt lens in sediment accumulated around CA), 34.45 ± 0.6 ka (40.9–37.7 ka; ^{14}C, OxA-10666 on burnt animal bone cemented to unburnt Neanderthal mandible SP59 in sediment accumulated around CA). CA entombed three articulated Neanderthal skeletons; an SP96 metacarpal bone gave a direct U-ser date of 54.1 ± 7.7 ka (APSLP1). Although not sampled in this study, they are in the Upper Cutting, where most teeth came from. Beneath the skeletons, a thin band of very firmly-cemented small stones (CB) seems to have been impervious enough as to cause sporadic water-logging with reducing conditions in gray overlying sediment and development in it of sheathed bacteria. The band sealed deeper sediments, now undergoing excavation that has reached 5 m below the rock roof, have provided abundant Mousterian and faunal remains (albeit no human ones). Several taxa are typical of the Iberian Late Pleistocene (*Equus caballus*, *Bos primigenius*, *Capra pyrenaica*, *Cervus elaphus*, *Lynx lynx*, *Oryctolagus cuniculus*, *Testudo hermanni,* etc.), whereas others occur that rapidly became locally extinct during the end of the Late Pleistocene (*Panthera pardus*, *Crocuta crocuta*, *Stephanorhinus* sp.*, Hippopotamus amphibius,* and *Hystrix javanica*). Pollen from the uppermost sediments indicates presence of pines and (absent today) moisture-dependent deciduous woodland, and thermophylls characteristic of southeastern Iberian and North Africa that do not regenerate after

frost (Carrión et al., 2003). Neanderthal teeth with carious lesions have been identified (Walker et al., 2011b). Teeth sampled for dental calculus come from excavated sediments (Upper Cutting) except for one (SP50) recovered from hillside rubble.

Kalamakia This Middle Paleolithic site is a cave on the western coast of the Mani Peninsula in the Peloponnese in southern Greece (36.469340, 22.420670). Archaeologists excavated Kalamakia from 1993 until 2006 (Harvati et al., 2009, 2013). Chronologists have dated basal deposits with U/Th radiometric dating to the MIS 5c transgression (109 + 14/−13 ka; De Lumley et al. 1994). Two of the five units produced substantial Middle Paleolithic remains (Units III and IV). Excavation concentrated on Unit IV due to hard breccia in Unit III. Seventeen occupation levels were identified in the sedimentary deposits of Unit IV. In addition to fauna and Mousterian lithics, 10 hominin teeth, crania and postcranial elements with diagnostic Neanderthal morphology were found, comprising of at least eight individuals, three of which we sampled for dental calculus (KAL 3, 5 and 8). Unit IV's youngest archaeological level has been dated to >39 ka (Harvati et al., 2013), placing KAL 5 and KAL 8 between MIS 5a (85–74 ka) and 39 ka. Excavators uncovered KAL 3 in Unit III, which overlies 5c beach rock and was truncated by sea transgressions in MIS 5a. Evidence of other truncations from sea transgressions from local caves implies that KAL 3 dates to the MIS 5b (Darlas, 2012). Faunal and palynological studies reveal that prevailing climatic local conditions were mild. Fallow deer (*Dama dama*) is particularly common in the assemblages, followed by ibex, wild pig (S*us scrofa*), red deer, tortoise and some modified seashell. Maquis shrubland and Mediterranean presteppic forest species covered the Peninsula (Lebreton et al., 2008). Extensive avian remains reveal evidence of tree cover in a predominantly open warm/temperate environment (Roger and Darlas, 2008).

Comparative data for model

We prepared data from past dental calculus studies for a comparative analysis (Salazar-García et al., 2013; Henry et al., 2014). This dataset included starch and phytolith counts from nine Middle Paleolithic sites but calculus from one of these sites (Sima de las Palomas del Cabezo Gordo) was also part of the main study. As other microremains are not included in previous published studies, we included only starch and phytoliths in our model. Our samples were weighed in mg; weights for all

eight sites are not available. In the datasets presented in this paper we treated starches of the same type that occurred as lumps as one starch, as accurately counting each starch in a lump is not possible. We collected the updated estimated date range for each site and used the median value.

Goyet This archaeological site comprises several caves near Gesves, in the Namur Province of Belgium. The cave system has seen several campaigns of excavation in the 19th and 20th century. Early explorers found hominin remains (Goyet VIII) in 1868 in the largest of the caves. Dupont found the studied mandible in the second of five fauna-rich levels (Dupont, 1872; Toussaint, 2006). Originally, the fossil was thought to be modern human due to its stratigraphic proximity to Aurignacian artefacts, but this has been re-evaluated and it now is accepted to be a Neanderthal (Rougier et al., 2012; Wißing et al., 2015). In addition, in the Aurignacian phase there is an upper Magdalenian level dated to 13 ka (Toussaint, 2006). Mixing is present in all levels and its date was long ambiguous but this has recently been re-evaluated as dating to 44–45.5 ka cal BP (Wißing et al., 2015). This date places the hominin in a transitional period. Regional vegetation reconstructions suggest the surrounding environment was generally tundra-steppe.

La Chapelle-aux-Saints This Middle Paleolithic site is located in the Corrèze region of southern France. Researchers have excavated La Chapelle-aux-Saints since 1905, and this has recovered evidence of Mousterian sediments and a complete Neanderthal in 1908. The chronological history of this site has been studied with electron spin resonance (ESR), suggesting dates of 56 ka or 47 ka depending on the radiation uptake model used (Grün and Stringer, 1991). The ESR may suggest the remains belong to the warm parts of MIS 3, but this contradicts correlation with the Combe-Grenal sequence which would put the remains at the end of MIS 4 and beginning of MIS 3. The associated fauna profile is predominately reindeer (*Rangifer tarandus*), with some bovines (*Bos*/*Bison* sp.), horse (*Equus* sp.), ibex (*Capra* sp.), wolf (*Canis lupus*), fox (*Canis vulpes*), cave hyena (*Crocuta spelaeaus*), boar (*Sus scrofa*), marmot (*Arctomys* sp.) and rhinoceros (Boule, 1911; Bouyssonie et al., 1913). The fauna is clearly a cold phase profile indicating a date during the late MIS 4 (Mellars, 1986). In addition, fauna shows the surrounding environment was a cold open biome.

La Ferrassie This site is located in the Vézère Valley, in the Dordogne region of France. La Ferrassie is a large deep cave with an adjoining long rock-shelter and

small rock-shelter. The site has a plethora of levels of different periods in various sections of the cave. Mousterian levels below the long rock-shelter produced remains of six Neanderthals in excavations during 1909 and 1921. The bison, auroch and red deer that dominate the Mousterian fauna imply a moderate temperate environment. These fauna suggest tree cover and a closed, forested environment (Capitan and Peyrony, 1912a, 1912b; Guérin et al., 2015). Mousterian deposits at La Ferrassie have been recently dated with OSL and radiocarbon dating, suggesting that the Neanderthal remains La Ferrassie 1 is most likely dates to 39 ± 5 ka and La Ferrassie 2 dates to 43 ± 3 ka (Guérin et al., 2015).

La Quina La Quina is a series of rock shelters in the Charente region of Central France. Remains used in this study were found in 1911 in one of two subsections of Station Amont, a deposit extending below the upper rock shelter base. This deposit was studied over the course of several excavations. Excavations revealed Mousterian remains, faunal debris and the remains of many Neanderthals (Henri-Martin, 1961). The upper deposits of the sequence at Station Amont are considered to date to 48-43 ka. This, combined with cold phase fauna, indicates a date for the fossil of MIS 4, probably 71– 57 ka (Debénath and Jelinek, 1998). Fauna found was mostly bovines, horse and reindeer, with few other species represented (Debénath and Jelinek, 1998). These fauna also suggest a cold and dry treeless environment.

Malarnaud This site is a cave in the Ariège region of Southern France. There has been scientific interest in the cave since 1883. Deposits dated to Mousterian, Aurignacian and Magdalenian have been found onsite. Investigators found a juvenile Neanderthal mandible during 1888 in the lower of two layers in a side chamber of this cave complex. However, it is possible that the mandible was moved by carnivores in this chamber as it is removed from much of the archaeological material. Unfortunately, the site has not been radiometrically dated. Faunal profiles indicate the mandible dates to Riss-Würm interglacial, 130–117 ka or the beginning of the Würm, 100–50 ka. Fauna in the layer of the mandibles include cave lion (*Panthera leo*), cave hyena, fox, and wolf, rhinoceros (Rhinocerotidae) and mammoth (Boule, 1889; Filhol, 1889). This fauna is suggestive of tree cover in the early glacial warm or transitional phase, and thus we classify the environment as of mixed openness.

Spy This archaeological site is located in Jemeppe-sur-Sambre, province of Namur in Belgium. The site was excavated from 1879 onwards, and the Neanderthal remains were found in a bone rich layer. Later excavations have clarified the

stratigraphy of the cave. Faunal profiles from excavation of this layer have suggested an intensely cold climate (Otte, 1979). Some studies found misclassified Neanderthal remains in faunal bags (Crevecoeur et al., 2010). These teeth were directly radiocarbon dated to about 36 ka (Semal et al., 2009). De Puydt and Lohest (1887) recovered fauna from this level, including horse and hyena, with some mammoth, woolly rhinoceros, reindeer, red deer, aurochs, cave bear, cave lion, wolf, wolverine (*Gulo gulo*) and badger (*Meles meles*). However, paleoenvironment reconstructions may be questioned due to the poor stratigraphic integrity of this layer (de Puydt and Lohest, 1887). The direct date of the hominin remains firmly place the occupation in a cold phase when dry tree landscapes dominated much of Europe. We consider the environment as open for our model.

Kůlna Cave This Middle Paleolithic site is located in the Moravian Karst, in the eastern part of the Czech Republic in Central Europe. The cave saw first investigations in 1880 when stone tools and bones of extinct animals were noticed (Sroubek et al., 2001). Karel Valoch conducted the first modern archaeological investigation in 1961 and 1976. He identified 14 sedimentary complexes covering the last interglacial to the Holocene. Neanderthal remains were found in strata 7a and 7c, but specimens in this study come from stratum 7a only. Radiocarbon dating has suggested a date of >45 ka BP ^{14}C, and electron spin resonance on layer 7a shows it dates to 50 ± 5 ka BP (Rink et al., 1996). The character of the fauna from this layer matches this age (Rink et al., 1996). Layer 7a contained reindeer, with mammoth and few elk. The presence of reindeer clearly indicate cold conditions of central Europe in the MIS 3 (Valoch, 1970).

Shanidar Cave This site is located in the Zagros Mountains in Northwest Iraq. Solecki and colleagues excavated the cave between 1952 and 1957. Excavators described four archaeological strata (A, B, C and D). The Shanidar III fossils were found in Mousterian level D (Solecki, 1960). A radiocarbon date near the Shanidar I fossil indicates that Shanidar III is >46 ka BP, possibly as old as 50 ka BP (Solecki, 1960). Goat (*Capra* sp.) and sheep (*Ovis* sp.) dominate fauna assemblages found on site. This reflects the local mountainous topography (Perkins, 1964; Evins, 1982). Pollen analysis indicated the presence of date palms (*Phoenix dactylifera*), walnuts (*Juglans* sp.), chestnuts (*Castanea* sp.), oaks (*Quercus* sp.) and herbs (Solecki, 1961; Leroi-Gourhan, 1968, 1969; Leroi-Gourhan and Arlette, 1975). These plant

taxa indicate a mild moist environment with at least some level of tree cover. For our model, we classified this habitat as closed.

Reference collection

Different approaches exist to microremain identification including cell anatomy based classification used in phytolith studies, qualitative identification used In starch studies or morphometric identification which is used for phytoliths and starches (Madella et al., 2005; Henry and Piperno, 2008; Power et al., 2015a, 2015b). We used cell anatomy classification when possible such as with phytoliths but for starches this is not possible. For starches we could not use morphometric identification as this depends on a complete reference collection of all major plant foods, and at this point this is not possible to deuce as a priori. Instead we used qualitative identification based on a reference collection of modern plant samples, including >2,000 global species. Our reference collection has extensive coverage of edible Western Eurasian species. From these species we identified over 54 edible and possibly edible species present in Pleistocene Eurasia that produced starches, and that might be represented in our samples. We identified phytoliths using available literature including PhyCore database (Albert et al., 2016). We did not make a reference collection for unsilicified plant microremains, as these microremains are unlikely to be diagnostic, nor do we currently have a sufficient reference collection for identifying types of microremains (Power et al., 2015b).

Starch grain identification

SEM studies of immature wheat grain show that the diagnosis lenticular type (type B) reaches its characteristic shape early in development, even at 4 days after anthesis these lenticular starches are typically smaller than mature starches but grow rapidly and may reach 12 µm after 10 days after anthesis assuming ripening at 52 days (Evers, 1971) . These immature grains may exhibit a more pronounced equatorial groove. Water content of immature wheat remains high late in grain development, suggesting that green grain approaching ripeness with large lenticular starches would still be doughy and chewable and suitable for consumption without complex processing. Spells of rain during the ripening period may also extend this period when the grain is water rich and chewable.

Supplementary references

Albert, R.M., Ruíz, J.A., Sans, A., 2016. PhytCore ODB: A new tool to improve efficiency in the management and exchange of information on phytoliths. Journal of Archaeological Science 68, 98–105.

Blanc, A.C., 1954. Reperti fossili neadertaliani nella Grotta del Fossellone al Monte Circeo: Circeo IV. Quaternaria 1, 171–175.

Boule, M., 1889. La caverne de Malarnaud, près Montseron (Ariège). Bulletin de la Société Philomathique de Paris 1, 83–86.

Boule, M., 1911. L'Homme fossile de La Chapelle-aux-Saints. Annales de Paléontologie 6, 106–172.

Bouyssonie, A., Bouyssonie, J., Bardon, L., 1913. La station Moustérienne de la "Bouffia" Bonneval a la Chapelle-aux-Saints. L'Anthropologie 24, 609–640.

Capitan, L., Peyrony, D., 1912a. Station préhistorique de La Ferrassie, commune de Savignac-du-Bugue (Dordogne). Revue Anthropologique 22, 50–99.

Capitan, L., Peyrony, D., 1912b. Trois nouveaux squelettes humains fossiles. Comptes rendus des séances de l'Académie des Inscriptions et Belles-Lettres 56, 449–454.

Crevecoeur, I., Bayle, P., Rougier, H., Maureille, B., Higham, T., van der Plicht, J., De Clerck, N., Semal, P., 2010. The Spy VI child: A newly discovered Neandertal infant. Journal of Human Evolution 59, 641–656.

Darlas, A., 2012. Geomorphologic evolution and occupation of the caves of the western Mani peninsula during the Upper Pleistocene and the Holocene. In: Zacharias, N., Georgakopoulou, M., Polykreti, K., Fakorellis, G., Vakoulis, T. (Eds.), Proceedings of the 5th Symposium of the Hellenic Society of Archaeometry. Papazisi, Athens, pp. 237–253.

De Lumley, H., Darlas, A., Anglada, R., Cataliotti-Valdina, J., Desclaux, E., Dubar, M., Falguères, C., Keraudren, B., Lecervoisier, B., Mestour, B., Renault-Miskovsky, J., Trantalidou, K., Vernet, J.L., 1994. Grotte de Kalamakia (Aréopolis, Péloponnèse). Bulletin de Correspondance Héllénique 118, 535–559.

de Puydt, M., Lohest, M., 1887. L'homme contemporain du Mammouth à Spy (Namur). In: de Radiguès de Chennevière, H. (Ed.), Fédération Archéologique et Historique de Belgique. Fédération archéologique et historique de Belgique, Namur, pp. 205–240.

Debénath, A., Jelinek, A.J., 1998. Nouvelles fouilles à La Quina (Charente) : Résultats préliminaires. Gallia Préhistoire 40, 29–74.

Devièse, T., Karavanić, I., Comeskey, D., Kubiak, C., Korlević, P., Hajdinjak, M., Radović, S., Procopio, N., Buckley, M., Pääbo, S., Higham, T., 2017. Direct dating of Neanderthal remains from the site of Vindija Cave and implications for the Middle to Upper Paleolithic transition. Proceedings of the National Academy of Sciences 114,

10606–10611.

Dupont, E., 1872. Les Temps Préhistoriques en Belgique: L'Homme pendant les Âges de la Pierre dans les Environs de Dinant-sur-Meuse. Murquardt, Brussels.

Evers, A.D., 1971. Scanning electron microscopy of wheat starch. III. Granule development in the endosperm. Starch - Stärke 5, 157–192.

Evins, M.A., 1982. The fauna from Shanidar Cave: Mousterian wild goat exploitation in northeastern Iraq. Paléorient 8, 37–58.

Filhol, M.H., 1889. Note sur une machoire humaine trouvée dans la caverne de Malarnaud près de Montseron (Ariège). Bulletin de la Société Philomathique de Paris 1, 69–82.

Follieri, M., Giardini, M., Magri, D., Sadori, L., 1998. Palynostratigraphy of the Last Glacial period in the volcanic region of central Italy. Quaternary International 47–48, 3–20.

Frayer, D.W., Fiore, I., Lalueza-Fox, C., Radovčić, J., Bondioli, L., 2010. Right handed Neandertals: Vindija and beyond. Journal of Anthropological Sciences 88, 113–127.

Grün, R., Stringer, C.B., 1991. Electron spin resonance dating and the evolution of modern humans. Archaeometry 33, 153–199.

Guérin, G., Frouin, M., Talamo, S., Aldeias, V., Bruxelles, L., Chiotti, L., Dibble, H.L., Goldberg, P., Hublin, J.-J., Jain, M., Lahaye, C., Madelaine, S., Maureille, B., McPherron, S.J.P., Mercier, N., Murray, A.S., Sandgathe, D., Steele, T.E., Thomsen, K.J., Turq, A., 2015. A multi-method luminescence dating of the Palaeolithic sequence of La Ferrassie based on new excavations adjacent to the La Ferrassie 1 and 2 skeletons. Journal of Archaeological Science 58, 147–166.

Harvati, K., Darlas, A., Bailey, S.E., Rein, T.R., El Zaatari, S., Fiorenza, L., Kullmer, O., Psathi, E., 2013. New Neanderthal remains from Mani peninsula, Southern Greece: the Kalamakia Middle Paleolithic cave site. Journal of Human Evolution 64, 486–99.

Harvati, K., Panagopoulou, E., Runnels, C., 2009. The paleoanthropology of Greece. Evolutional Anthropology 18, 131–143.

Henri-Martin, G., 1961. Le niveau de Chatelperron a la Quina (Charente). Bulletin de la Société Préhistorique Française 58, 796–808.

Henry, A.G., Brooks, A.S., Piperno, D.R., 2014. Plant foods and the dietary ecology of Neanderthals and early modern humans. Journal of Human Evolution 69, 44–54.

Henry, A.G., Piperno, D.R., 2008. Using plant microfossils from dental calculus to recover human diet: a case study from Tell al-Raqā'i, Syria. Journal of Archaeological Science 35, 1943–1950.

Higham, T.F.G., Ramsey, C.B., Karavanić, I., Smith, F.H., Trinkaus, E., 2006. Revised direct radiocarbon dating of the Vindija G1 Upper Paleolithic Neandertals. Proceedings of the National Academy of Sciences of the United States of America 103, 553–557.

Higham, T., Karavanić, I., Comeskey, D., Kubiak, C., Korlević, P., Hajdinjak, M., Radović, S.,

Procopia, N., Buckley, M., Pääbo, S., Higham, T., 2017. Direct dating of Neanderthal remains from the site of Vindija Cave and implications for the Middle to Upper Paleolithic transition. Proceedings of the National Academy of Sciences of the United States of America 114, 10606–10611.

Howell, F.C., 1957. The evolutionary significance of variation and varieties of “Neanderthal” The Quarterly Review of Biology 32, 330–347.

Karavanić, I., Smith, F.H., 1998. The Middle/Upper Paleolithic interface and the relationship of Neanderthals and early modern humans in the Hrvatsko Zagorje, Croatia. Journal of. Human Evolution 34, 223–248.

Krings, M., Capelli, C., Tschentscher, F., Geisert, H., Meyer, S., von Haeseler, A., Grossschmidt, K., Possnert, G., Paunović, M., Pääbo, S., 2000. A view of Neandertal genetic diversity. Nature Genetics 26, 144–146.

Kuhn, S.L., 1991. “Unpacking” reduction: Lithic raw material economy in the Mousterian of west-central Italy. Journal of Anthropology Archaeology 10, 76–106.

Lebreton, V., Psathi, E., Darlas, A., 2008. Environnement vegetal des neandertaliens de la Grotte deKalamakia (Aréopolis, Grèce). In: Darlas, A., Mihailovi, D. (Eds.), The Palaeolithic of the Balkans. Proceedings of the XV UISPP World Congress. BAR International Series 1819, Oxford, pp. 61–68.

Leonard, C., Vashro, L., O’Connell, J.F., Henry, A.G., 2015. Plant microremains in dental calculus as a record of plant consumption: a test with Twe forager-horticulturalists. Journal of Archaeological Science Reports 2, 449–457.

Leroi-Gourhan, A., 1968. Le Neanderthalien IV de Shanidar. Bulletin de la Société Préhistorique Française 65, 79–83.

Leroi-Gourhan, A., 1969. Pollen grains of Graminae and Cerealia from Shanidar and Zawi Chemi. In: Ucko, P.J., Dimbleby, G.W. (Eds.), The Domestication and Exploitation of Plants and Animals. Aldine Transaction, Chicago, pp. 141–148.

Leroi-Gourhan, A., Arlette, 1975. The flowers found with Shanidar IV, a Neanderthal burial in Iraq. Science 190, 562–564.

Madella, M., Alexandre, A., Ball, T., 2005. International code for phytolith nomenclature 1.0. Annals of Botany 96, 253–260.

Mallegni, F., 1992. Human remains (Fossellone 3; ex Circeo 4) referable to *Homo s. neanderthalensis* from Fossellone Cave (Monte Circeo, Latium, Italy). Rivista De Antropologia 70, 217–227.

Martinson, D.G., Pisias, N.G., Hays, J.D., Imbrie, J., Moore, T.C., Shackleton, N.J., 1987. Age dating and the orbital theory of the ice ages: Development of a high-resolution 0 to 300,000-year chronostratigraphy. Quaternary Research 27, 1–29.

Mauch Lenardić, J., 2014. Bank vole *Myodes* (=*Clethrionomys*) *glareolus* (Schreber, 1780):

Rare species in the Late Pleistocene fauna of Croatia. Quaternary International 328–329, 167–178.

Mellars, P., 1986. A new chronology for the French Mousterian period. Nature 322, 410–411.

Otte, M., 1979. Le Paléolithique Supérieur Ancien en Belgique. Musees Royaux d'Art et d'Histoire, Bruxelles.

Perkins, D., 1964. Prehistoric fauna from Shanidar, Iraq. Science 144, 1565–1566.

Radmilli, A. M., 1962. La Piccola Guida Della Preistoria Italiana. Istituto Italiano di Prehistoria e Protostoria, Florence.

Power, R.C., Salazar-García, D.C., Straus, L.G., González Morales, M.R., Henry, A.G., 2015a. Microremains from El Mirón Cave human dental calculus suggest a mixed plant-animal subsistence economy during the Magdalenian in Northern Iberia. Journal of Archaeological Science 60, 39–46.

Power, R.C., Salazar-García, D.C., Wittig, R.M., Freiberg, M., Henry, A.G., 2015b. Dental calculus evidence of Taï Forest chimpanzee plant consumption and life history transitions. Scientific Reports 5, 15161.

Rink, W.J., Schwarcz, H.P., Valoch, K., Seitl, L., Stringer, C.B., 1996. ESR dating of Micoquian industry and Neanderthal remains at Kůlna Cave, Czech Republic. Journal of Archaeological Science 23, 889–901.

Roger, T., Darlas, A., 2008. Upper-Pleistocene bird remains from Kalamakia Cave. In: Darlas, A., Milhailović, D. (Eds.), The Palaeolithic of the Balkans. Proceedings of the XV UISPP World Congress. BAR International Series 1819, Oxford, pp. 69–76.

Rougier, H., Crevecoeur, I., Beauval, C., Bocherens, H., Flas, D., Germonpré, M., Semal, P., Van der Plicht, J., 2012. New data from an old site : Neandertals at Goyet (Belgium) and their mortuary behavior. American Journal of Physical Anthropology 147, 252–253.

Salazar-García, D.C., Power, R.C., Sanchis Serra, A., Villaverde, V., Walker, M.J., Henry, A.G., 2013. Neanderthal diets in central and southeastern Mediterranean Iberia. Quaternary International 318, 3–18.

Schwarcz, H.P., Schoeninger, M.J., 1991. Stable isotope analyses in human nutritional ecology. American Journal of Physical Anthropology 34, 283–321.

Semal, P., Rougier, H., Crevecoeur, I., Jungels, C., Flas, D., Hauzeur, A., Maureille, B., Germonpré, M., Bocherens, H., Pirson, S., Cammaert, L., De Clerck, N., Hambucken, A., Higham, T., Toussaint, M., Van der Plicht, J., 2009. New data on the late Neandertals: Direct dating of the Belgian Spy fossils. American Journal of Physical Anthropology 138, 421–428.

Sergi, S., 1954. La mandibola neandertaliana Circeo II. Rivista di Antropologia 41, 305–344.

Smith, F.H., Boyd, D.C., Malez, M., 1985. Additional upper Pleistocene human remains from Vindija cave, Croatia, Yugoslavia. American Journal of Physical Anthropology 68, 375–

383.

Solecki, R.S., 1960. Three adult Neanderthal skeletons from Shanidar cave, northern Iraq. Annual Report of the Board of Regents of the Smithsonian Institution,603–635.

Solecki, R.S., 1961. New anthropological discoveries at Shanidar, northern Iraq. Transactions of the New York Academy of Sciences 23, 690–699.

Solecki, R.S., 1963. Prehistory in Shanidar Valley, Northern Iraq. Science 139, 179–193.

Sroubek, P., Diehl, J.F., Kadlec, J., Valoch, K., 2001. A Late Pleistocene palaeoclimate record based on mineral magnetic properties of the entrance facies sediments of Kulna Cave, Czech Republic. Geophysical Journal International 147, 247–262.

Stiner, M.C., Kuhn, S.L., 1992. Subsistence, technology, and adaptive variation in Middle Paleolithic Italy. American Anthropologist 94, 306–339.

Toussaint, M., 2006. Research in the caves of Goyet (Gesves, Province of Namur, Belgium). In: Demarsin, B., Otte, M. (Eds.), Neanderthals in Europe. ERAUL, Liege, pp. 115–134.

Trinkaus, E., 2014. The Shanidar Neandertals. Academic Press, New York.

Trinkaus, E., Walker, M. J., 2017. The People of Palomas: Neandertals from the Sima de las Palomas del Cabezo Gordo, Southeastern Spain. Texas A&M University Press, Austin.

Valoch, K., 1970. Early Middle Palaeolithic (Stratum 14) in the Kulna Cave near Sloup in the Moravian Karst (Czechoslovakia). World Archaeology 2, 28–38.

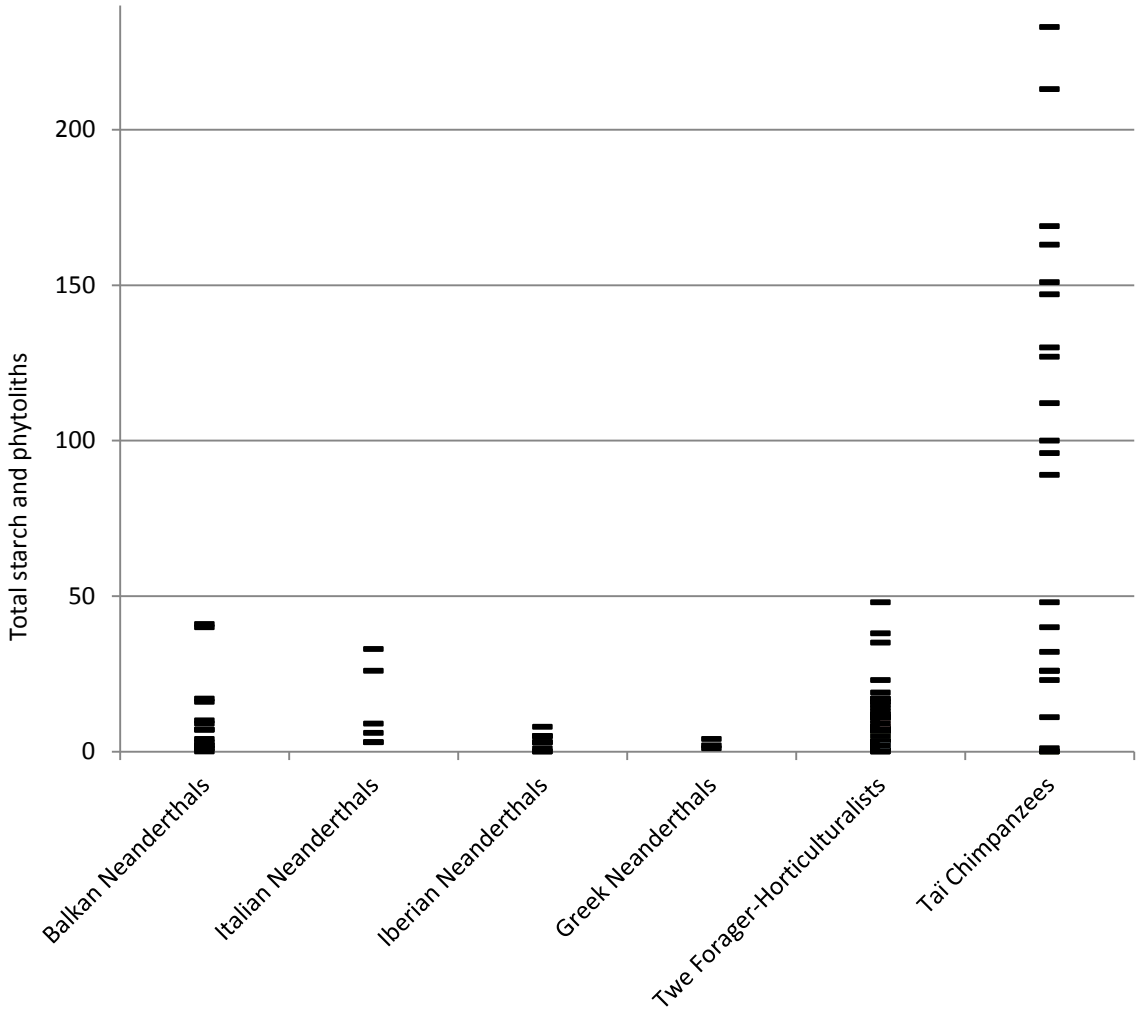
van Andel, T.H., Tzedakis, P.C., 1996. Palaeolithic landscapes of Europe and environs, 150,000-25,000 years ago: An overview. Quaternary. Science Reviews 15, 481–500.

Vitagliano, S., Piperno, M., 1991. Lithic industry of level 27 Beta of the Fossellone cave (S. Felice Circeo, Latina). Quaternaria Nova 1, 289–304.

Vogel, J.C., Waterbolk, H.T., 1963. Groningen radiocarbon dates IV. Radiocarbon 5, 163–202.

Wild, E.M., Paunović, M., Rabeder, G., Steffan, I., Steier, P., 2001. Age determination of fossil bones from the Vindija Neanderthal site in Croatia. Radiocarbon 43, 1021–1028.

Wolpoff, M.H., Smith, F.H., Malez, M., Radovčić, J., Rukavina, D., 1981. Upper Pleistocene human remains from Vindija cave, Croatia, Yugoslavia. American Journal of Physical Anthropology 54, 499–545.



SOM Figure S1. Total numbers of starch and phytoliths in each Neanderthal site with reference groups: Twe forager-horticulturalists from Namibia and Taï forest chimpanzees from Côte d'Ivoire, from Leonard et al., (2015) and Power et al., (2015), respectively.

Table S1

Dental calculus results for the various studied localities, in Excel format.

Table S2

List of starch types and their identification criteria. Small is <10 μm, moderate is 10–20 μm, and large is >20 μm.

Type	Description
Type 1	Moderate size, spherical-subspherical, with thick lamellae, some show yellow coloration, simple, may be cracked, diameter is 10–22 μm.
Type 2	Large circular-subcircular in 2D, some have thick lamellae, some have yellow coloring, spherical-lenticular-subspherical 3D, simple, monomodal, diameter is 20=>μm.
Type 3	Rounded polyhedral/ sub-polyhedral, 2 or more facets but more of surface is not covered by facets, facets often are less sharply defined, no lamellae. Cross arms are clear and straight, May be large, which is suggestive of damage.
Type 4	Slightly eccentric, simple, monomodal starch.
Type 5	Faceted, generic type. Sub polyhedral. Monomodal, simple.
Type 6	Ovoid starch, with or without surface features, some have damaged central cavity but this is not a classification trait. Simple. Monomodal
Type 7	Triangular-elliptical-hemispherical, may have central fissure, other surface features can include lamellae.
Type 8	Lenticular or subelliptical in 3D, equatorial groove may be visible, some show signs of gelatinization, distinguished from type 17 by poorly defined longitude crack. Identified as legume
Type 9	Small oval or slight ovoid, subspherical (5–10 μm), 1–2 facets may be apparent, few surface features but a central aperture may be present.
Type 10	Large ovoid, routinely eccentric, often with lamellae, diameter is >40 μm.
Type 11	Large spherical/subspherical, monomodal, simple starch, >20 μm.
Type 12	Very small polyhedron, no lamellae or fissures (showing some possible *Avena* sp. or bogbean features but not identified).
Type 13	Very small simple starch with centric cross. Monomodal.
Type 14	Large sub polyhedral, simple, lamellae may be present. 15 μm or above. Monomodal.
Type 15	Isolated, lenticular or subelliptical in 3D, well preserved equatorial groove, some show signs of gelatinization, but preservation varies. Type is consistent with Type A Triticeae starches, often occurring with Type B Triticeae starches, size distribution is bimodal. Identified as ancient starch
Type 16	Polyhedral shape only, aggregating type, some have cracks emerging from central cavity decay, monomodal, moderate size, diameter is 8–25 μm. Hard endosperm starch.
Type 17	Very eccentric and gelatinized starch. Too damaged to classify or identify.
Type 18	Small, round, constrained facets may be present, possible central hilum opening, no other discernible surface features, diameter is <10 μm. Morphologically redundant.
Type 19	Morphologically redundant starch, simple, polyhedral starch.
Type 20	Lenticular or subelliptical in 3D, occurs in aggregates, well preserved equatorial groove, excellent preservation, large or moderate size, consistent with small Type A Triticeae starches, bimodal, often

	occurring with Type B Triticeae starches. Identified as possibly modern due to fresh condition and found in groups.
Type 21	Slightly eccentric, simple, monomodal starch, cf. Black bindweed (*Fallopi*a sp.).
Type 22	Highly eccentric, simple, large size. Very elongate. cf. true lily (*Lilium* sp.).
Type 23	Two tightly compound grains, with the juncture between the two unclear. The overall shape is ovoid, while each grain is hemispherical. The hila are centric and unmarked. Redundant.

Table S3

GLM Input and contamination controls, in Excel format.

Table S4

Summary of coefficients of statistical models.

Model	Term	Estimate	Std. Err.	Z value	*p*
Tests of effect of tree cover, ET and age on microremain diversity					
Random effect negative Binomial model	Intercept	-0.106	0.807	-0.132	0. 894
	Mixed tree cover	0.567	0.849	0.667	0. 504
	Open tree cover	0.897	0.539	1.662	0.096
	ET	-0.031	0.285	-0.108	0.913
	Age of fossil specimen	9.88	9.168	1.077	0.28
	Intercept	-0.101-1.159	0.8023.574	-0.125-3.671	0.8990.0002
Random effect negative Binomial Model with alternative chronology	LowMixed tree cover	-0.009-1.313	0.9136.695	-0.009-1.962	0.9920.049
	MixedLow tree cover	0.7469.394	0.5362.816	1.3903.3352	0.1640.0008
	Alternative age of fossil specimenET	-0.0283.11	0.2861.113	-0.1002.798	0.9199 0.005
	Alternative age of fossil specimenET	0.1908.510	0.2942.411	0.6483.528	0.5160.0004

Table S5

Results of pairwise comparison

	Chapelle-aux-Saints	Ferrassie	Fossellone	Goyet	Guattari	Kulna	Malarnaud	Quina	Sima
Ferrassie	1.00E-05	—	—	—	—	—	—	—	—
Fossellone	3.10E-10	1	—	—	—	—	—	—	—
Goyet	1.10E-07	1	1	—	—	—	—	—	—
Guattari	4.50E-10	1	1	1	—	—	—	—	—
Kulna	0.00012	1	1	1	1	—	—	—	—
Malarnaud	2.50E-05	2.50E-16	<2e-16	<2e-16	<2e-16	1.00E-14	—	—	—
Quina	1	3.20E-06	3.20E-10	5.30E-08	4.50E-10	2.90E-05	0.01975	—	—
Sima	2.50E-09	1	1	1	1	1	<2e-16	2.00E-09	—
Vindija	1.10E-08	1	1	1	1	1	<2e-16	7.50E-09	1