

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

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29

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31

32 **Abstract**

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

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

59

60 **Introduction**

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

69 2009; O'Connell, 2006). This idea is supported by stable isotopic and fauna data
70 (Stiner, 1999; Richards et al., 2001; Conard et al., 2011). In this view, Neanderthal
71 subsistence was reliant on a more restricted range of staples than that of modern
72 humans, giving them a competitive disadvantage against Upper Paleolithic peoples.

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

84 Neanderthals are often interpreted as narrow spectrum foragers (Kuhn and
85 Stiner, 2006; O'Connell, 2006; Stiner and Kuhn, 2009; Stiner, 2013). Models of
86 Middle Paleolithic dietary ecology suggest that they hunted predominantly medium
87 and large prime-age fauna with only infrequent use of small mammals, and aquatic
88 and plant foods. Nitrogen stable isotope ratios indicate that they were at the top of
89 the terrestrial food web and obtained most of their protein from medium and large-
90 sized herbivores (Richards et al., 2000; Lee-Thorp and Sponheimer, 2006; Richards
91 and Trinkaus, 2009; Wißing et al., 2015). Some zooarchaeologists have argued that
92 this diet was stable over time, with little evidence of a chronological trend towards
93 more diverse resource use (Stiner et al., 2000; Stiner, 2013). Surviving tool
94 repertoires show scant evidence for the investment in specialized technology for
95 collecting plants, fish, and small mammals (Kuhn and Stiner, 2006; O'Connell, 2006;
96 Henry et al., 2014). A low diversification in food choice and high consumption of
97 large and medium-sized game matches evidence from site density and their genetic
98 history that imply sparse, dispersed populations of Neanderthals that did not deplete
99 high-ranked prey items (Stiner, 1999; Stiner and Munro, 2002; Macdonald et al.,
100 2009; Verpoorte, 2009; Castellano et al., 2014).

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

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

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

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

137 Douara Cave (Matsutani, 1987) in the Levant, and Gorham's and Vanguard Cave in
138 Gibraltar (Barton et al., 1999; Gale and Carruthers, 2000)—suggest some level of
139 plant use. The most comprehensive studies of dietary variability that incorporate
140 plant foods stem from indirect evidence, such as dental microwear analyses, which
141 have revealed that Neanderthals predominantly consumed meat, with a possible
142 increased use of plants in the southern wooded parts of their range (El Zaatari et al.,
143 2011; Fiorenza et al., 2011). The microwear of Neanderthals who inhabited cold-
144 steppe environments resembled that of historic Fuegians who inhabited cold wet
145 scrublands (Grine, 1986; Fiorenza et al., 2011). However, dental wear is silent on the
146 number and types of plants consumed, or if low-ranked foods were consumed,
147 meaning these studies create an incomplete picture of diet in different environments.

148 Neanderthals appear to have had more diverse diets in southern regions,
149 possibly due to ecological variation (Stiner, 1999, 2001). Some researchers have
150 pointed to legume assemblages from Kebara Cave (63–45 ka) and grass seed
151 phytoliths from Amud Cave (70–55 ka), arguing that the use of more diverse
152 resources was present already in the Middle Paleolithic (Madella et al., 2002; Lev et
153 al., 2005). Others have studied starch and phytolith microremains trapped in dental
154 calculus, and found that Neanderthal dental calculus from sites such as Spy and
155 Shanidar indicate the use of date palm fruits and grass seeds in the Levant, and
156 water lily tubers in northern Europe (Henry et al., 2011). In addition, geneticists have
157 explored dental calculus aDNA as a source of dietary information, although plant
158 DNA was found, its sheer rarity makes its significance hard to clarify (Weyrich et al.,
159 2017). Despite these insights into Neanderthal use of plants, these samples are too
160 widespread in time and space to give reasonable coverage of potential variation in
161 Neanderthal diets. Importantly, these studies tell us little about the longevity of the
162 Middle Paleolithic dietary niche. It is unknown if Neanderthal exploitation of plant
163 foods broadened over the hundreds of thousands of years they occupied Eurasia in
164 response to higher populations or milder climates, similarly to what is observed for
165 the Upper Paleolithic and recent hunter-gatherers, or if variation is only linked to
166 different environments.

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

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

190

191 **Materials and methods**

192 *Sites and samples*

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

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

217

218 *Dental calculus and control sampling*

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

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

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

241 To minimize risk of contamination from airborne modern plant material and
242 laboratory supplies (Langejans, 2011; Crowther et al., 2014; Henry, 2014), we
243 conducted a regime of weekly laboratory cleaning. All laboratory work surfaces were
244 cleaned with hot water, washed with starch-free soap and with 5% sodium hydroxide
245 (NaOH). To assess contamination types, we additionally performed wipe tests before
246 and after weekly cleaning to quantify starch and other contaminants. Wipe tests
247 retrieved settled particles of the surface area (74 x 43 cm²) of the laboratory positive-
248 pressure laminar flow hood used for mounting. Results of these intensive
249 contamination control tests are found in the SOM Table S1.

250

251 *Sample preparation and mounting*

252 Using standard procedures (Power et al., 2014; Leonard et al., 2015), each
253 sample was weighed and transferred to microcentrifuge tubes while in a clean
254 laminar flow hood at the Plant Food Group Laboratories at the MPI-EVA. Each
255 sample was then gently broken up with one second of micropestle use in a 1.5 ml
256 Eppendorf microcentrifuge tube containing ~30 µl of a 25% glycerine solution to
257 reduce sample loss due to static electricity. The samples were then centrifuged at
258 1691× g (Heraeus MEGAFUGE 16 with TX-400 fixed Rotors) for 10 minutes. These
259 samples were mounted on glass slides and examined under brightfield and cross-
260 polarized light on a Zeiss Axioscope microscope at 400× magnification. No
261 decalcification treatment (HCl or EDTA) was used, in order to avoid additional
262 processing steps that might remove or destroy microremains, particularly calcium
263 oxalates. This leaves lumps of calculus but microremains still entrapped could be
264 easily seen by adjusting focal plane. Identifying microremains embedded in situ was
265 considered advantageous as it provided information on their origin. Studies on the
266 effects of grinding on starches suggest that the gentle grinding used in this sample
267 preparation method would have little impact on starches (Henry et al., 2009).

268

269 *Identification and classification*

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

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

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

293

294 *Taphonomic biases*

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

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

314

315 *Converting microremain diversity into measures of dietary breadth*

316 Estimating dietary breadth from animal and plant remain assemblages is a
317 major challenge in archaeological research (Grayson and Delpech, 1998). Until
318 recently, there were no data on whether dental calculus could in any way reflect
319 dietary breadth. Fortunately, recent experimental studies have shown that dental
320 calculus assemblages can reflect a significant amount of dietary breadth and have
321 laid a foundation on which to base expectations (Leonard et al., 2015; Power et al.,
322 2015b).

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

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

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

347

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

349 It is long established that the percent of diet derived from plants and terrestrial
350 meat is strongly related to climate (Kelly, 1995), and it is expected that this applies to
351 plant species used as well (Ichikawa and Terashima, 1996). Thus, we envisaged that
352 there is a strong relationship between climate and the taxonomic breadth of plant
353 food use in forager societies. Foragers in grassland environments are known to
354 follow this pattern (Marean, 1997). A second major aspect of this study was
355 examining the link between the dietary reliance on plant foods and the number of
356 different types of plant taxa in a variety of environments, as it might be possible that
357 ancient foragers might be highly reliant on plant foods but consume only a small
358 number of taxa. The study aimed to provide verification that recent foragers, who rely
359 on a greater amount of plant food, gather a greater range of plant species than
360 foragers who use fewer plants. Due to the lack of non-grassland datasets on the
361 number of plant species consumed by foragers, we tested if there is a relationship by
362 plotting number of plant species documented as food items in ethnographic forager
363 diets of the Labrador Inuit, Yupik, Aleutians, Ona, Ojibwa, Hadza, Alyawara, !Kung
364 and Baka (Table 4; Fig. 2; Smith, 1932; Ager and Ager, 1980; O'Connell et al., 1983;
365 Hattori, 2006; Veltre et al., 2006; Marlowe, 2010; Clark, 2012; Berihuete-Azorín,
366 2013; Crittenden and Schnorr, 2017). Although the data are sparse, the slope
367 highlights that in warm climates, where plant foods are more important, foragers
368 exploit a higher number of species. If Neanderthals behaved like modern humans,
369 then we should also expect a climate-based variation in the number of plant species
370 they consumed.

371

372 *Paleotemperature and paleoenvironment reconstruction*

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

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

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

$$402 \quad ET = [(18 * MST) - (10 * MWT)] / (MST - MWT + 8)$$

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

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

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

416

417 *Statistical analyses*

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

427 To calculate approximate sample size needed, we used Poisson regression
428 power analysis in GPower 3.1 (Demidenko, 2007; Faul et al., 2009). The duration
429 (defined as 'Mean exposure') 2.666 °C, as the dataset as a whole varies by 2.66°C
430 with two tails, with a 'Base rate $\exp(\beta_0)$ ' that is estimated to be 5.75. Based on the
431 results from the modern foragers (Fig. 2), we estimated a 12.6% increase in MBUs
432 for every 1°C of effective temperature and we assigned a power of 0.85 at $\alpha = 0.05$.
433 The resulting simulation revealed mean power values of 0.856 for a sample size of
434 42, although less than our sample size of 58 it is more than the number of samples
435 from individual Neanderthals (37).

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

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

457

458 **Results**

459 *Contamination controls*

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

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

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

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

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

498

499 *Dental calculus microremain assemblages and dietary breadth*

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

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

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

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

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

549 Grotta Guattari and Grotta Fossellone We examined the calculus from the right lower
550 third molar of Grotta Guattari II and the lower first molars (right and left), and a lower
551 second incisor of Grotta Guattari III. Calculus samples from the five teeth from Grotta
552 Guattari produced high numbers of microremains and microremain types. A total of
553 151 microremains were found in the dental calculus of the five teeth (SOM Table
554 S1). Phytoliths and starches were classified into a similar, but lesser number of
555 minimum botanical units as Vindija. Absolute minimum botanical units varied from 1
556 to 7 (Table 3; SOM Text S1).

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

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

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

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

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

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

601

602 *Dietary flexibility and dietary niche stability*

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

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

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

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

636

637 **Discussion**

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

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

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

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

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

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

690 Some of the types that we were able to identify tell us about Neanderthal
691 dietary behavior. In particular, many of the microremains come from foods that are
692 often considered low-ranked, like grass seeds and tubers (Simms, 1985; Kelly,
693 1995). Grass seeds used at Vindija and at Grotte Guattari demonstrate an
694 investment in a low-rank plant food in cool habitats of the northern Balkans and
695 coastal Italy. The use of grass seeds is often linked to terminal Pleistocene
696 Southwest Asian foragers, who invested in broad spectrum diets because grass
697 seeds are usually costly to harvest and prepare for consumption (Simms, 1985). On
698 the other hand, there is abundant evidence that groups like the Vindija Neanderthals
699 were big game hunters and that energetic contribution from plants is not likely to
700 have rivaled that of meat. Grass seeds are widely used by recent foragers in warm
701 and cool environments (Lothrop, 1928; Simms, 1985; Harlan, 1989; Brand-Miller and
702 Holt, 1998). Middle Paleolithic foragers probably only used grass seed as a limited
703 component of the broader plant diet as this resource offers limited nutritional return
704 (Simms, 1985). This is the pattern observed in Upper Paleolithic human foragers of
705 Southwest Asia, where grass use is most prominent (Savard et al., 2006; Rosen,
706 2010).

707 It is unclear if Neanderthals gradually used a more diverse array of plants,
708 alongside the modest increase in Neanderthal population from 70 ka onwards (Foley
709 and Lahr, 2003; van Andel and Davies, 2003; Speth and Clark, 2006). If a
710 chronological trend in vegetal dietary breadth is absent, it agrees with the lack of a
711 trend in their predation niche before 55 ka. Although we cannot test if Neanderthal
712 vegetal dietary breadth diverged from an overwhelmingly dominant hunting
713 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

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

752

753 **Conclusions**

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

765 Plant foods were likely valued for their micro- or macronutrient profiles rather
766 than caloric energy alone. Hominin physiology limits the total dietary protein intake,
767 impeding an absolute reliance on protein-rich foods such as terrestrial mammals
768 (Cordain et al., 2000; Speth, 2010; Hockett, 2012). Recent foragers have avoided
769 the effects of protein overconsumption by incorporating other macronutrients into
770 their diet. Evidence from recent foragers worldwide suggests sourcing animal fat was
771 a preeminent strategy for offsetting risk of protein poisoning (Speth and Spielmann,
772 1983; Cordain et al., 2000). However, obtaining concentrated sources of animal fat
773 from a diet of terrestrial ungulates may not have always been possible. Triticeae,
774 Fabaceae and Liliaceae offer rich sources of carbohydrates that may have offset the
775 problems of lean protein consumption.

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

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

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

799

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1182

1183 **Figure legends**

1184

1185 **Figure 1.** Map of western Eurasia with the studied sites indicated.

1186

1187 **Figure 2.** The relationship between warmer environments and effective temperature.
1188 Although only a limited amount of data are available, our survey includes samples

1189 from polar, temperate, tropical and arid climates. Data available in Table 4. $R^2 =$
1190 0.885.

1191

1192 **Figure 3.** The minimum botanical units of starch and phytoliths from Neanderthal
1193 calculus, fauna calculus and control sediments demonstrate that Neanderthal dental
1194 calculus samples show a distinct signal indicating they reflect hominin diet. Each
1195 circle represents an individual sample.

1196

1197 **Figure 4.** Mosaic of a small selection of microremains and comparative modern
1198 reference plant matter. Each scale bar represents 10 μm . Images give examples of
1199 microremain types and do not show identification criteria. For information on
1200 identification criteria and reference collection see SOM S1 (Table 3; SOM S1 Table
1201 S2). (a–b) Starch from Vindija Neanderthal identified as Triticeae under bright field
1202 and cross polarized light. (c–d) A reference Triticeae starch (*Triticum turgidum*.)
1203 under bright field and cross polarized light. (e–f) Plant matter with several ovoid
1204 starches resembling *Lilium* bulb starches under bright field (e) and (f) cross polarized
1205 light. (g–h) Reference bulb starches of *Lilium* sp. under bright field (g) and cross
1206 polarized light (h) in GTNIII. (i–j) Polyhedral starch under bright field (i) and cross
1207 polarized light (j). (k) Spore of *Pteridium* sp. (l) Diatom embedded in calculus. (m)
1208 Fragment of grass leaf. (n) Triporate Betulaceae pollen. (o) Unsilicified tracheid plant
1209 tissue.

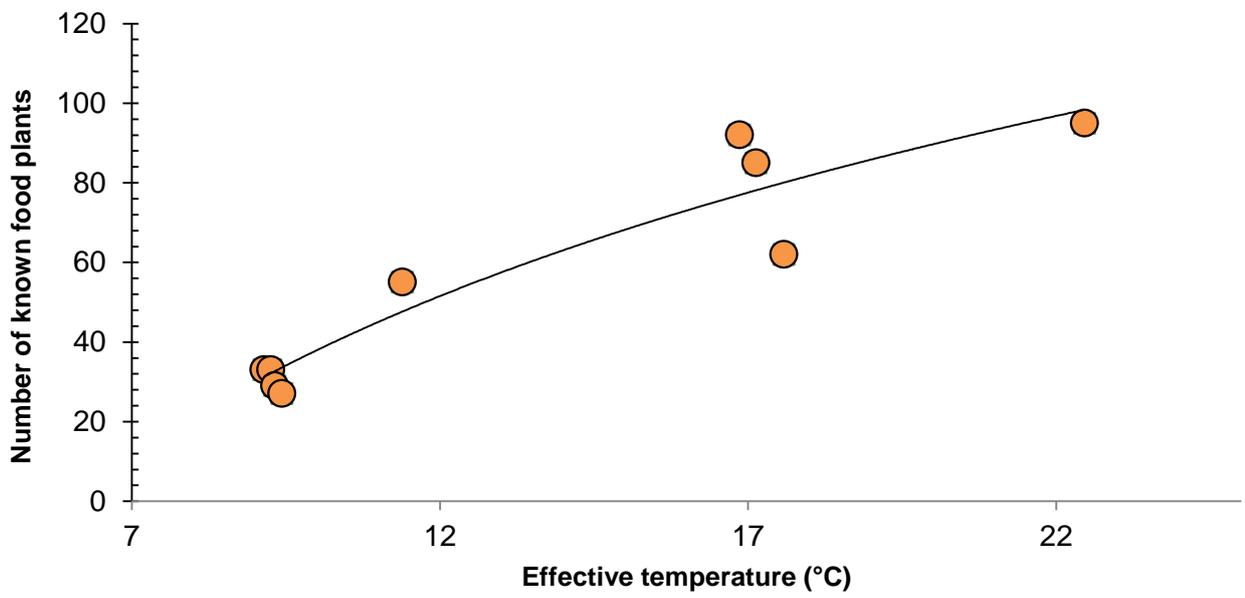
1210

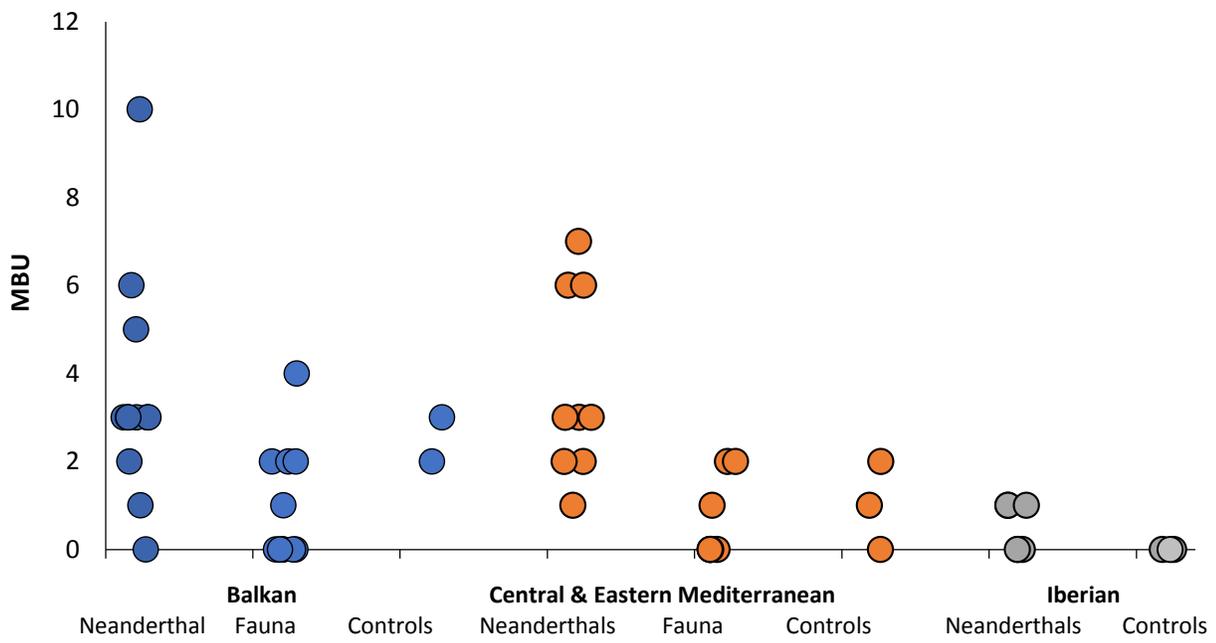
1211 **Figure 5.** A minimum botanical unit index of the starch and phytoliths from
1212 Neanderthal dental calculus shows that warmer climates are not associated with
1213 increased diversity. Samples are from Neanderthal remains presented in this study,
1214 as well as Salazar-Garcia et al. (2013) and Henry et al. (2014). Each dot represents
1215 an individual sample.

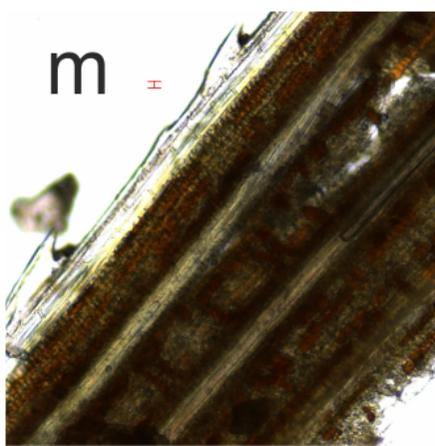
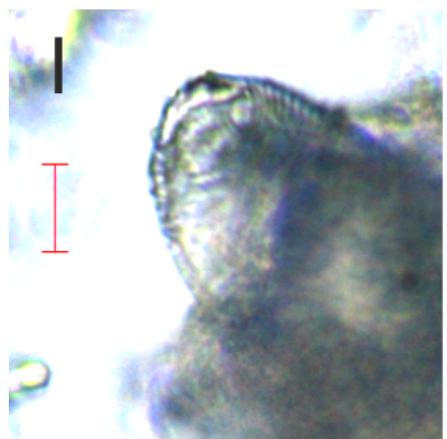
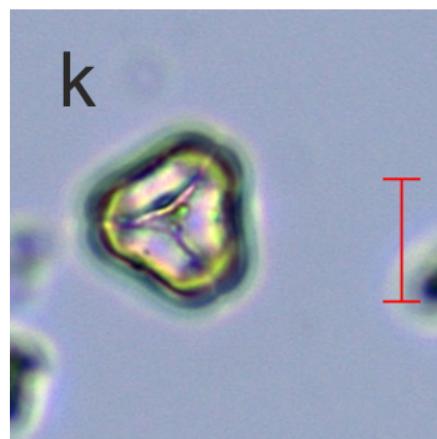
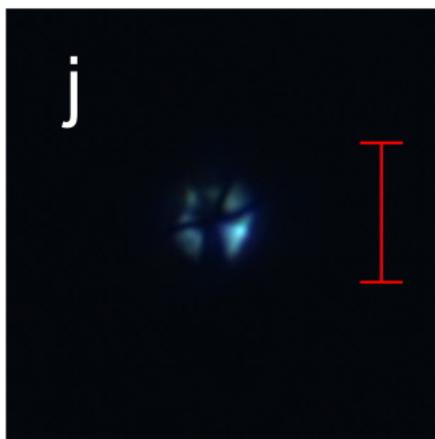
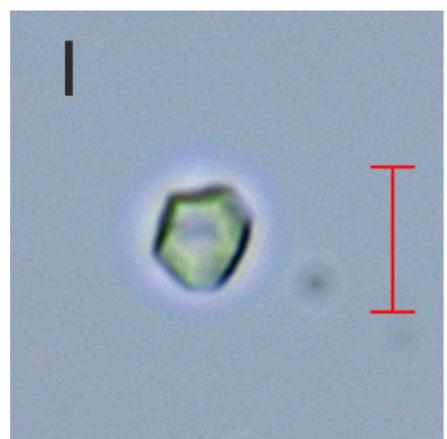
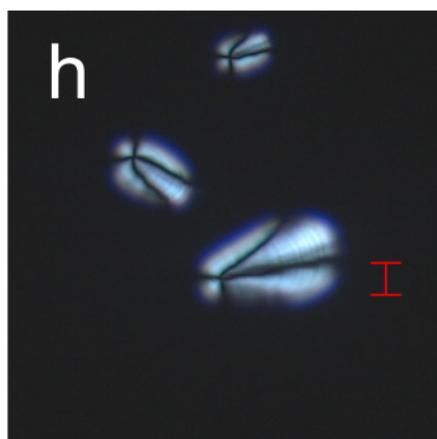
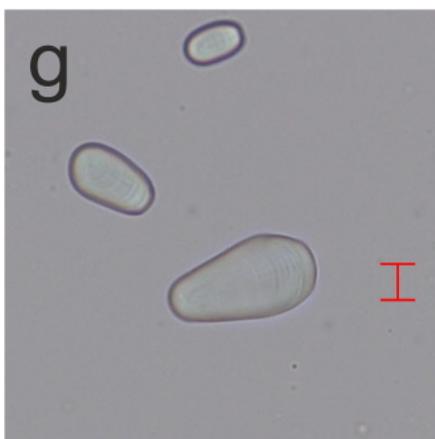
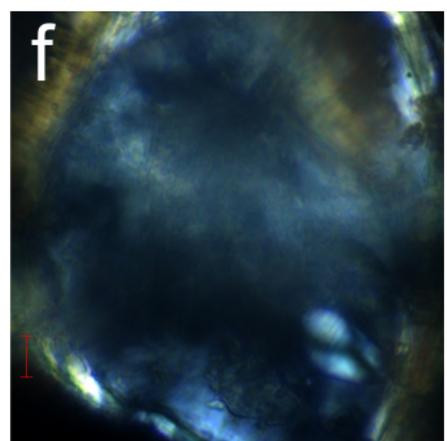
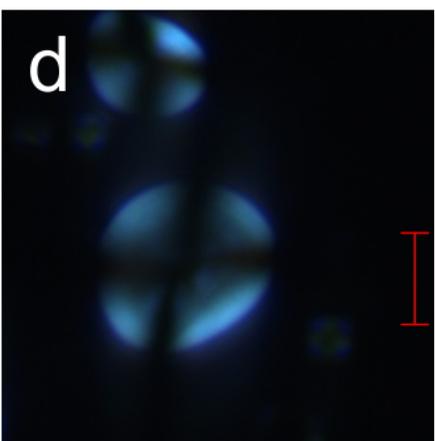
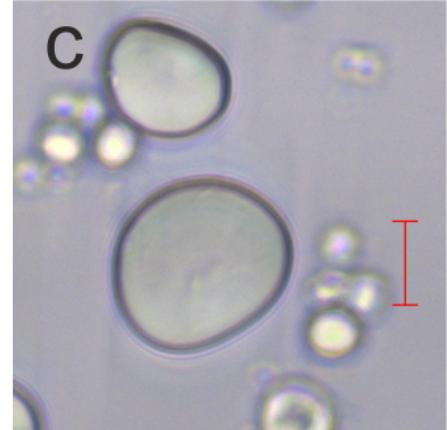
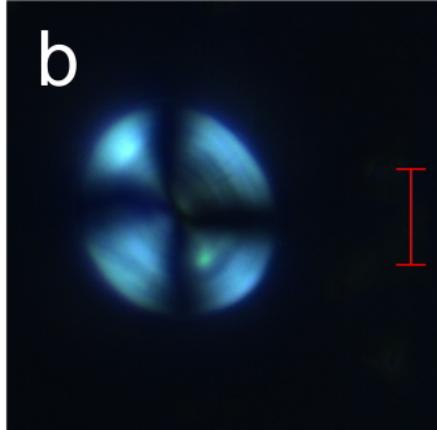
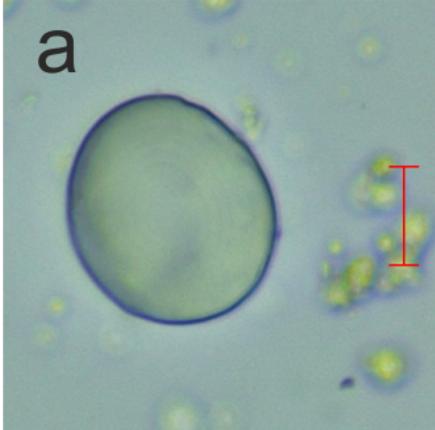
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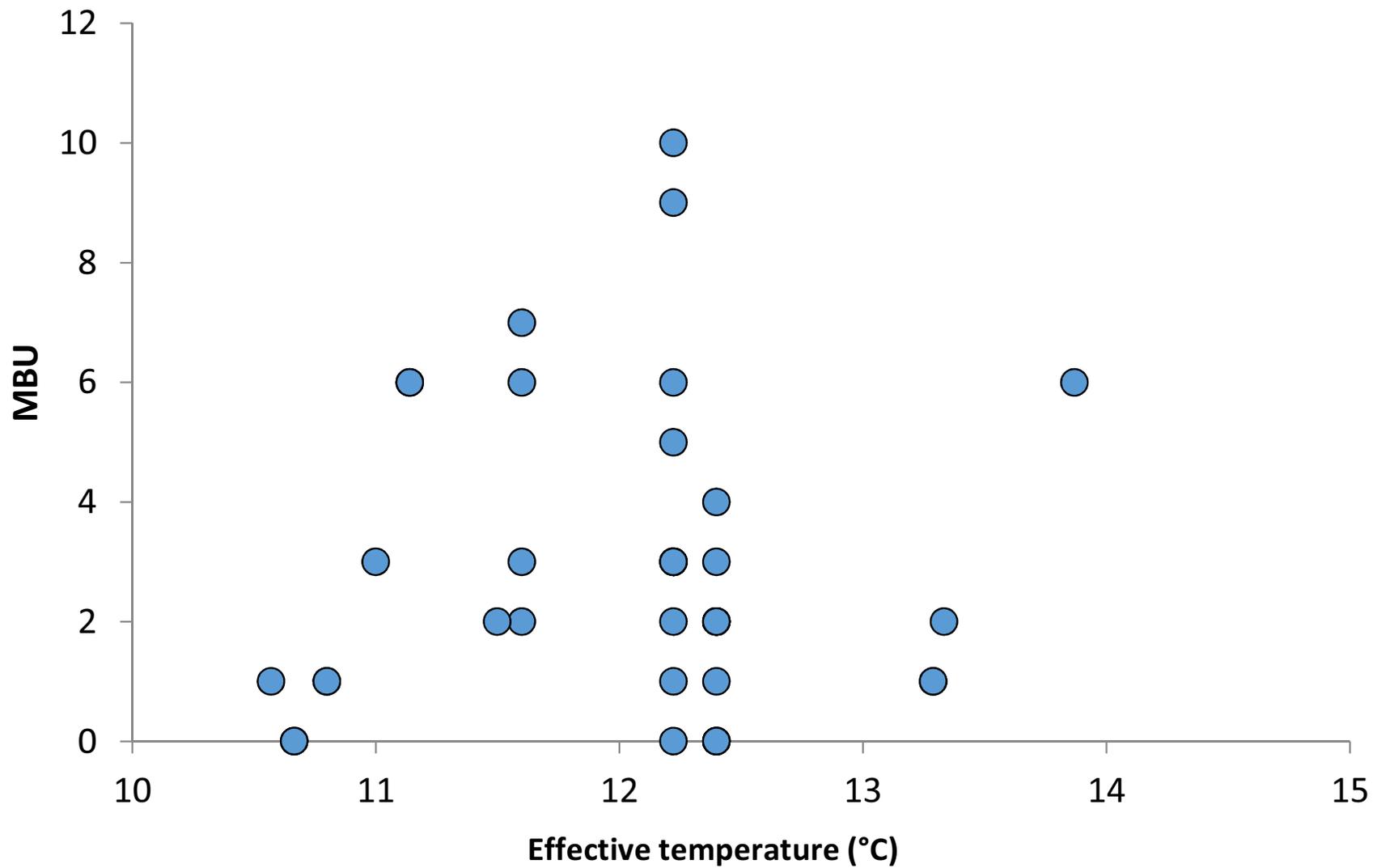


- Dental calculus samples analyzed in past studies
- Dental calculus samples analyzed in this study









1 **Table 1**

2 Analyzed Neanderthal dental calculus from Vindija, Grotta Guattari, Grotta
 3 Fossellone, Sima de las Palomas del Cabezo Gordo and Kalamakia. Site ages are
 4 reported in Table 4. Multiple samples from the same individual are presented as a
 5 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	—

8 **Table 2**

9 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
Kúlna	Kúlna 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

10

11 ^a Site age is calculated by using the mean of the calendric ages.

12 ^b Tree cover is calculated with pollen and fauna data.

13 ^c Paleotemperature is calculated from the Stage Three Project dataset.

14 ^d ET= effective temperature (which is a measure of biologically relevant temperature).

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

16

17

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)	<i>Celtis/ Boehmeria/ Morus or Urtica</i>
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	Poaceae
		Parallelepipedal	
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. <i>Fallopia</i> sp.)	Multicellular polyhedrons	Dicot leaf
Type 22	Cf. <i>Lilium</i> 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 Plate Calcium oxalate	Dicot leaf Dicot leaf/fruit Plant

21

22

23 **Table 4**

24 Relationship between effective temperature and the number of taxa in the diet of
 25 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

26

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

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

31

32

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

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; Devière 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 tangle 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 m² 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; ¹⁴C, OxA-15423 on burnt lagomorph bone in burnt lens in sediment accumulated around CA), 34.45 ± 0.6 ka (40.9–37.7 ka; ¹⁴C, 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*, *Crocota 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 (*Sus 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 spelaeus*), 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 ¹⁴C, 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 deduce 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.

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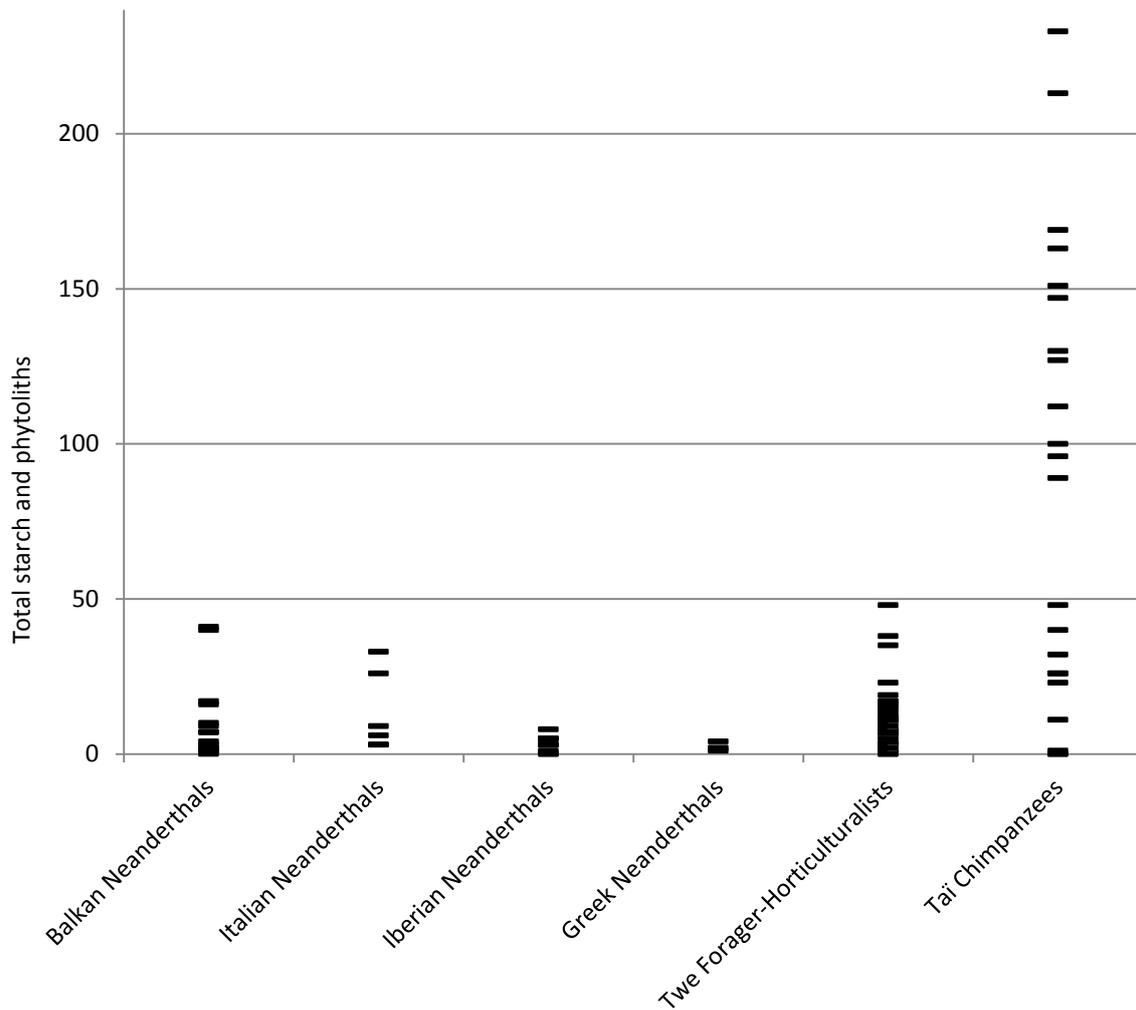
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SOM Figure S1. Total numbers of starch and phytoliths in each Neanderthal site with reference groups: Two forager-horticulturalists from Namibia and Tai forest chimpanzees from Côte d'Ivoire, from Leonard et al., (2015) and Power et al., (2015), respectively.

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-sub-spherical, 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-sub-spherical 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, sub-spherical (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/sub-spherical, monomodal, simple starch, >20 µm.
Type 12	Very small polyhedron, no lamellae or fissures (showing some possible <i>Avena</i> 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 (<i>Fallopia</i> sp.).
Type 22	Highly eccentric, simple, large size. Very elongate. cf. true lily (<i>Lilium</i> 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	<i>p</i>
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
Random effect negative Binomial Model with alternative chronology	Intercept	-0.101	0.8023.5	-0.125	0.8990.
		1.159	74	3.671	0002
	LowMixed tree cover	-0.009	0.9136.6	-0.009	0.9920.
		1.313	95	1.962	049
	MixedLow tree cover	0.7469.394	0.5362.8	1.3903.	0.1640.
			16	3352	0008
	Alternative age of fossil specimenET	-0.0283.11	0.2861.1	-	0.9199
		13	0.1002.	0.005	
			798		
	Alternative age of fossil specimenET	0.1908.510	0.2942.4	0.6483.	0.5160.
			11	528	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