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Plant foods and the dietary ecology of Neanderthals and early modern humans

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ABSTRACT

One of the most important challenges in anthropology is understanding the disappearance of Neanderthals. Previous research suggests that Neanderthals had a narrower diet than early modern humans, in part because they lacked various social and technological advances that lead to greater dietary variety, such as a sexual division of labor and the use of complex projectile weapons. The wider diet of early modern humans would have provided more calories and nutrients, increasing fertility, decreasing mortality and supporting large population sizes, allowing them to out-compete Neanderthals. However, this model for Neanderthal dietary behavior is based on analysis of animal remains, stable isotopes, and other methods that provide evidence only of animal food in the diet. This model does not take into account the potential role of plant food. Here we present results from the first broad comparison of plant foods in the diets of Neanderthals and early modern humans from several populations in Europe, the Near East, and Africa. Our data comes from the analysis of plant microremains (starch grains and phytoliths) in dental calculus and on stone tools. Our results suggest that both species consumed a similarly wide array of plant foods, including foods that are often considered low-ranked, like underground storage organs and grass seeds. Plants were consumed across the entire range of individuals and sites we examined, and none of the expected predictors of variation (species, geographic region, or associated stone tool technology) had a strong influence on the number of plant species consumed. Our data suggest that Neanderthal dietary ecology was more complex than previously thought. This implies that the relationship between Neanderthal technology, social behavior, and food acquisition strategies must be better explored.

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Introduction

The dietary behavior of Neanderthals has frequently been tied to explanations of their extinction. Results from faunal profiles (e.g., [Stiner, 2006](#); [Stiner et al., 2000](#)), nitrogen and carbon isotope analyses (e.g., [Bocherens, 2009](#); [Richards and Trinkaus, 2009](#)), and energy requirement estimations (e.g., [Froehle and Churchill, 2009](#)), together with a lack of complex technology (e.g., [Shea, 2006](#)), have suggested that Neanderthals ate almost exclusively large animal game, with very little contribution from plants, small game or

aquatic foods. In a behavioral ecology context, this narrow diet is a reflection of an environment where encounter rates with highly-ranked prey are high, human population sizes are low, and the pressure to create new, complex social structures, such as a sexual division of labor, and complex technology to increase the capture and processing of foods, such as atlatls and dedicated plant grinding implements, is low ([Bright et al., 2002](#); [Kuhn and Stiner, 2006](#); [O'Connell, 2006](#)).

In contrast, analyses of modern human diets have suggested that their dietary breadth has increased through time, beginning in the African Middle Stone Age (MSA). These groups consumed more marine and fish resources ([Drucker and Bocherens, 2004](#); [Marean et al., 2007](#); [McBrearty and Brooks, 2000](#); [Richards et al., 2001](#); [O'Connor et al., 2011](#)), developed specialized technologies, such as complex projectile weapons and fishing ([Yellen et al., 1995](#);

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Brooks et al., 1995, 2006; O'Connor et al., 2011), and possibly a more sophisticated social organization, with a sexual division of labor (Kuhn and Stiner, 2006) that allowed them to acquire a wider variety of food more efficiently.

Based on these perceived dietary differences, several authors have suggested that the interaction between Neanderthals and modern humans would have been strongly influenced by their food acquisition strategies and related behaviors (Hockett and Haws, 2005; Kuhn and Stiner, 2006; O'Connell, 2006; Shea and Sisk, 2010). In these views, the foraging intensity of modern humans constrained the Neanderthals in the pursuit of their own subsistence strategies. In short, both groups competed for the same large game, but modern humans had two benefits: reduced costs associated with hunting due to their complex technology, and the ability to get more kinds of food, including lower-ranked plant foods, due to their social structure. This would have provided them with not only more calories per unit of land, but also a more balanced nutrition and concomitant reduced maternal and infant mortality, leading to increased population sizes (Hockett and Haws, 2005). Between competitive pressure from modern human groups and a worsening climate during the Last Glacial (Müller et al., 2011), Neanderthals may have been unable to obtain enough calories by focusing on diminishing supplies of large game, and this may have contributed to their extinction.

This view of Neanderthal and early modern human diet and behavior has recently been challenged on several fronts. First, detailed analyses of both Neanderthal dental microwear (El Zaatari et al., 2011) and dental mesowear (Fiorenza et al., 2011) have suggested more variation within Neanderthal diets than previously expected. In both cases, Neanderthal groups living in southern and wooded environments had dental wear more similar to that of modern forager groups that consume a variety of foods, while Neanderthals in more northern and dry environments had diets similar to modern forager groups that consume predominantly meat. These results suggest that a simplistic view of a single 'Neanderthal diet' is no longer supportable. Second, a study investigating the effects of a diet limited to large, terrestrial herbivores on the health of pregnant Neanderthals argues that such a diet would kill the fetus and the female (Hockett, 2012), and concludes that Neanderthals must have consumed a wider variety of foods. Finally, the main methods used to support the idea of a nearly-carnivorous Neanderthal diet, nitrogen isotope values and faunal studies, provide minimal information about plant food. Nitrogen isotope values in particular can be misleading. First, because of the complex nonlinear relationship between food source and consumer, it is not possible to accurately estimate the proportion of meat versus plants in the diet, since large changes in the percentage of meat are indicated only by small increases in $\delta^{15}\text{N}$ values (Ambrose et al., 2003; Hedges and Reynard, 2007). Second, unlike herbivores that acquire all of their protein from plant leaves, foraging humans usually eat plants for their carbohydrate content, and therefore focus on the starch- and sugar-rich storage organs of plants, such as USOs and seeds (Lee, 1979; Marlowe, 2010). These storage organs may have higher nitrogen values (Hedges and Reynard, 2007), and in any case provide a smaller amount of protein to the body and are therefore relatively swamped by the meat protein signal. All of these new data suggest we must know more about Neanderthal consumption of plant foods in order to accurately reconstruct their diets.

We currently know surprisingly little about plants in Neanderthal diets. Though plants would likely have been available in Neanderthal environments (Hardy, 2010), there are few records of their use of plants. Charred seeds have been found in the Mousterian levels of Kebara (Lev et al., 2005) and Gorham's Cave (Barton et al., 1999). Phytoliths from edible plants have been recovered

from sediments in several Near Eastern Neanderthal sites (Henry et al., 1996, 2004; Albert et al., 1999, 2000; Rosen, 2003). More direct evidence for Neanderthal use of plants comes from studies of residues on stone tools from several sites in France (Hardy and Moncel, 2011; Hardy et al., 2013), and from the study of residues in dental calculus from El Sidron, Spain (Hardy et al., 2012). However, none of these studies have documented Neanderthal plant use across their range of environments and many are limited in their application, either providing only indirect evidence of plant use (plant remains in sediments) or giving limited or no information about which exact species were consumed (tool and tooth residue analysis).

The record of plant foods eaten by early modern humans prior to about 20 thousand years ago (ka) is only marginally better, with a few studies suggesting the use of starchy plants in the Middle Stone Age (>50 ka) at Ngalue, Mozambique (Mercader, 2009) and in the Sai Island, Sudan (Van Peer et al., 2003). In Europe, starchy plants, and particularly the roots of cattails (*Typha* spp.), were used by about 30 ka in Italy, Russia and the Czech Republic (Revedin et al., 2010). Starch grains and other plant residues have been recovered from stone tools from Aurignacian sites dating to just prior to 30 ka in Germany (Hardy et al., 2008), but these plant residues have not been identified to taxon.

Though these studies suggest that plants may have been important to both Neanderthals and modern humans, there has been to date no systematic exploration of plant use by these groups. In this paper, we focus on Neanderthal and modern human samples from several different geographic areas and time periods, and to document the taxa and types of plants consumed. Furthermore, we test several of the logical outcomes of the model that posits a narrow, meat-only diet for Neanderthals. If Neanderthals did have a limited, narrow diet that included only large game and also lacked a sexual division of labor, then they would have had fewer man-hours available for gathering and processing plant foods. Optimal foraging theory defines a narrow diet as one that includes only a few food types, which have the lowest cost-to-benefit ratio (usually measured in calories lost in pursuing and processing the food compared to calories gained), and are thus called 'high-ranked' foods. This means that in a fitness landscape where the best evolutionary strategy is for the whole group to pursue high-ranked game, then lower-ranked foods such as plants would be excluded from the diet. Thus we predict that Neanderthals consumed fewer plant species than did modern humans. Second, certain plant foods, such as grains and tubers, are often considered lower-ranked than others, because they require significant processing to make them edible (e.g., Gremillion, 2004). In the case that Neanderthals did consume plant foods, we predict they would focus only on high-ranked plant foods that require little processing.

In addition to the model that suggests dietary differences based on species (i.e., whether an individual is Neanderthal or modern human), there are several other factors that might influence the consumption of plant foods. Several authors have suggested that significant technological and behavioral shifts, including an increase in dietary breadth, occurred among modern human populations with the transition between the Middle and Upper Paleolithic in Eurasia and the Middle and Later Stone Age in Africa (e.g., Mellars, 2005; Steele and Klein, 2009). If these shifts did occur, then we would expect an increase in the number of plant foods consumed by later modern human populations. We predict, therefore, that earlier (Middle Stone Age and Middle Paleolithic) modern human groups consumed fewer plant foods than later modern human groups. Second, plant food availability should vary considerably by geographic region. Studies of modern foragers document a cline in plant food consumption, with groups living in tropical latitudes consuming more plant foods than those in

temperate or arctic latitudes (Kelly, 1995). Studies of Neanderthal dietary behavior have also suggested that ecogeographic factors influence dental microwear and mesowear (El Zaatari et al., 2011; Fiorenza et al., 2011). We predict that the geographic region from which samples came should also influence plant food consumption.

We tested these predictions by examining direct evidence for plant food consumption by a variety of a Neanderthal and modern human individuals and groups. Our results do not support any of the predictions, and suggest that new models for Neanderthal, as well as early modern human, diets must be drawn.

Materials and methods

Plant microremains are microscopic remnants of plants that preserve taxon-specific morphology. They can be recovered from a variety of archaeological contexts, and have been used to explore plant use in a variety of time periods across human history (Henry and Piperno, 2008; Henry et al., 2011; Pearsall et al., 2004; Zarrillo and Kooyman, 2006; Piperno and Dillehay, 2008; Yang et al., 2009; Revedin et al., 2010; Wesolowski et al., 2010).

We examined the microremains preserved in 209 samples from 30 populations from 20 sites in the Near East, Europe and Africa. These samples included representatives of Middle Paleolithic (MP) Neanderthals, Middle Paleolithic/Middle Stone Age (MP/MSA) modern humans, and Upper Paleolithic/Later Stone Age (UP/LSA) modern humans, and spanned the period between c.130–10 ka, with a few outliers (Table 1; SOM Table 1).

Starch grains and phytoliths were collected from dental calculus and stone tool residues using methods slightly modified from those described previously (SOM Text; Henry and Piperno, 2008; Henry et al., 2011). Every microremain was photographed, described using the terminology of the International Code for Starch Nomenclature (ICSN, 2011), and the International Code for Phytolith Nomenclature (Madella et al., 2005), and assigned to a 'type'. Each type was defined by having a shared unique, diagnostic morphology, and probably represented a single plant taxon. Unique microremains and those that were too damaged or encrusted with calculus to confidently assign to established types were counted singly as unique types. Where possible, the types were identified to plant taxon, usually at the family or tribe level, but occasionally to the genus or species, based on comparison with our modern reference collection and to published literature (e.g., Reichert, 1913; Seidemann, 1966).

We performed several controls for contamination, including using clean sampling methods, and testing the storage and sampling material (SOM Text). Several diagenetic and taphonomic processes, such as burial environments and curation practices, may have affected the survival of starch grains on our samples (Henry, 2014). We also recognize that not all consumed plants are represented as microremains in calculus (Leonard et al., 2013), and are thus missing from this analysis. However, we have no reason to expect that these processes would differentially affect our samples, thus making a directional bias in microfossil counts and represented types unlikely.

We then performed qualitative and quantitative analyses of the recovered microfossils. For the qualitative analysis, we assigned each calculus or stone tool sample to a hominin population. Populations were defined by their sharing the same stratigraphic context within a site (e.g., all of the Mousterian stone tools from Shanidar were one population, the teeth from Shanidar III were another, and all of the sampled teeth from La Ferrassie I and II were a third). We used these populations to ease descriptive comparisons of microfossil use, though we recognize that these populations subsume large and unequal amounts of time and possibly represent

palimpsests of environmental conditions, and that other groupings could have been made.

The quantitative analysis was divided into two parts. The first was a simple comparison of the number of microfossil types between populations. For each population, we counted the total number of recovered microfossils across all samples and the total number of types represented across all samples. The number of microfossil types roughly correlates with dietary breadth, or overall number of plant species that population consumed. However, because the number of types increases as the sample size increases (Grayson, 1984), we calculated Menhinick's index, a measure of species richness that accounts for sample size, which is commonly used in ecological studies (Magurran, 2004). The formula is S/\sqrt{N} , where S is the number of species (in this case, the number of microremain types in the population), and N is the total number of individuals (in this case, the total number of microremains in the population). By comparing the Menhinick's indices among our populations, we are able to look for patterns in diet breadth across these samples.

Finally, we ran two generalized linear mixed models (GLMM) (Baayen et al., 2008) on our data. The GLMMs are designed to examine what predictors or factors most strongly influence a response variable, while accounting for random effects. Based on the previous work described above, we predict that the number of microfossil types (a measure of dietary breadth) found on a sample was a function of the hominin species (Neanderthal or modern human) that sample came from, the associated stone tool technology (MP/MSA or UP/LSA), and/or geographic region (Europe, Near East, or Africa). Though we acknowledge that there may have been interactions among these variables, because of our data structure we were not able to include the interactions in the model (i.e., there are no Neanderthals from Africa). Because we expected stone tools and dental calculus to preserve microfossils in different manners, we ran separate models for the teeth and for the tools. Since we know that the number of microfossil types increases with the number of recovered microfossils, we weighted each sample's contribution to the model by the number of microfossils found on that sample. Prior to running the model, we checked the distribution of the number of microfossils and as a consequence, we z-transformed the number of microfossils. Furthermore, we expected that the age of a sample might have some influence on the number of microfossil types, so we included the age of the site as a control factor. In the stone tool model, we expected that the stone tool type (e.g., blade, flake, cobble) also influenced the number of microfossils and microfossil types recovered, so we included tool type as a control factor. Because our samples came from only a few of the known hominin sites, and because we had several samples from each site so not all samples could be assumed to be independent, we included the site as a random factor and the interaction between site and number of microfossils as a random slope. In the dental calculus model, because we occasionally had more than one sample from each individual (e.g., Shanidar III) and therefore not all samples could be assumed to be independent, we included individual as a random factor and the interaction between individual and number of microfossils as a random slope.

We fitted the model in R (R Development Core Team, 2011) using the function `glmer` of the R package `lme4` (Bates et al., 2011), with Poisson error structure and log-link function. We ran d fbeta-like tests for model stability, individually excluding each sample in the tools model, and individually excluding each individual in the teeth model (since there were several individuals with more than one sample). These tests suggested the presence of some influential cases, but when these cases were removed the significance of the final models did not change. Variance Inflation Factors (the function `vif` from the R package `car`, (Fox and Weisberg, 2011)) run on the two models with no random factors indicated that collinearity among the predictors was potentially an issue. This is unsurprising

Table 1
Populations included in this study.

	Population	Max age (ka)	Min age (ka)	Samples within pop.	Number of microremains	Number of types	Identified types	Menhinick's index	Species	Tech.	Area.	
Neanderthal only	Arcy-sur-Cure (Grotte des Fées) calculus	?	?	1	0	0		0.00	N	MP/MSA	E	
	Goyet 8 calculus	41	40	1	1	1		1.00	N	MP/MSA	E	
	Kůlna calculus	50	40	4	19	7	Triticeae	1.61	N	MP/MSA	E	
	La Chapelle-aux-Saints isolated molar calculus	68	60	1	0	0		0.00	N	MP/MSA	E	
	La Ferrassie I and II calculus	74	68	8	2	2		1.41	N	MP/MSA	E	
	La Quina tools	71	48	8	41	14	Triticeae, AP grass	2.19	N	MP/MSA	E	
	La Quina V calculus	71	57	3	3	3	?USO, ? Triticeae	1.73	N	MP/MSA	E	
	Malarnaud calculus	100	50	1	0	0		0.00	N	MP/MSA	E	
	Spy I and II calculus	37	36	4	136	48	Nymphaeae (USO), AP grass	4.22	N	MP/MSA	E	
	Sites with both species	Abri des Merveilles Mousterian tools	49	39	7	15	10	Triticeae, AP grass	1.44	N	MP/MSA	E
Abri des Merveilles Gravettian tools		27	25	8	10	7	Triticeae, AP grass	2.21	H	UP/LSA	E	
Gorham's Cave Mousterian tools		47	33	16	17	12	Triticeae, AP grass	2.91	N	MP/MSA	E	
Gorham's Cave Upper Paleolithic tools		18	11	7	15	10	Triticeae, AP grass, USO	2.43	H	UP/LSA	E	
Shanidar III calculus		50	46	3	96	46	Palm, <i>Hordeum</i> (Triticeae), USO, ?Fabeae	4.77	N	MP/MSA	NE	
Shanidar Mousterian tools		100	44	32	35	21	Triticeae, AP grass, USO, ? Fabeae	3.55	N	MP/MSA	NE	
Shanidar Upper Paleolithic tools		33	27	21	84	48	Triticeae, USO	5.24	H	UP/LSA	NE	
Modern human only		Abri Pataud N°2 calculus	22	20	5	6	4	USO	1.63	H	UP/LSA	E
		Blombos layer BBC1 calculus	99	70	2	3	3	AP grass	1.73	H	MP/MSA	A
		Blombos layer BBC2 calculus	99	70	3	41	14	AP grass	2.19	H	MP/MSA	A
	Cro Magnon 2 calculus	28	22	1	1	1		1.00	H	UP/LSA	E	
	Ishango 15, 16, 24 calculus	20	20	6	16	8	Triticeae, AP grass, USO	2.24	H	UP/LSA	A	
	Ishango 17 and 23A calculus	10	8	2	5	5	Triticeae, AP grass	2.00	H	UP/LSA	A	
	Klasies River Shelter 1B layer 10 calculus	102	98	1	6	5	Triticeae, ?USO	2.04	H	MP/MSA	A	
	Klasies River Shelter 1B layer 10 tools	102	98	9	14	10	AP grass	2.27	H	MP/MSA	A	
	Klasies River Cave 1 layer 14 calculus	102	98	9	14	10	Triticeae, AP grass, ?USO	2.67	H	MP/MSA	A	
	Klasies River Cave 1 layer 14 tools	102	98	14	34	20	Triticeae, AP grass, ?USO	3.43	H	MP/MSA	A	
	La Madeleine (Lartet and Christy) calculus	13	13	2	1	1		1.00	H	UP/LSA	E	
	Predmostí 21 and 26 calculus	27	26	4	0	0		0.00	H	UP/LSA	E	
	Skhul II, V, VI and VII calculus	130	100	6	15	7	Palm, ?Triticeae	1.81	H	MP/MSA	NE	
	Skhul tools	130	100	26	100	51	Palm, Triticeae, AP grass, USO	5.10	H	MP/MSA	NE	

Key: A question mark indicates reduced confidence in the identification. H = early modern human; N = Neanderthal; MP/MSA = Middle Paleolithic or Middle Stone Age; UP/LSA = Upper Paleolithic or Later Stone Age; E = Europe; NE = Near East; A = Africa. Dates, technology, and taxonomy were collected from the literature and are presented, along with details on exact samples, in the supplementary information. AP grass indicates a starch that may be from the seeds of grass in the Andropogoneae or Paniceae tribes. See text for details.

given the strong relationships between geographic location, species and associated technology, and was deemed to be an acceptable level of collinearity. Overdispersion was not an issue (tools: $\text{chisq} = 60$, $df = 82$, $p = 0.963$; teeth: $\text{chisq} = 17.5$, $df = 30$, $p = 0.58$), suggesting that the results can be trusted. We established the significance of the full model as compared with the null model

(comprising the intercept, the control factor, and the random factors) using a likelihood ratio test (R function *anova* with argument *test* set to 'Chisq').

In both quantitative analyses, we chose not to count those samples for which we recovered no microfossils. We recognize that the failure to find microfossils could be either a true representation

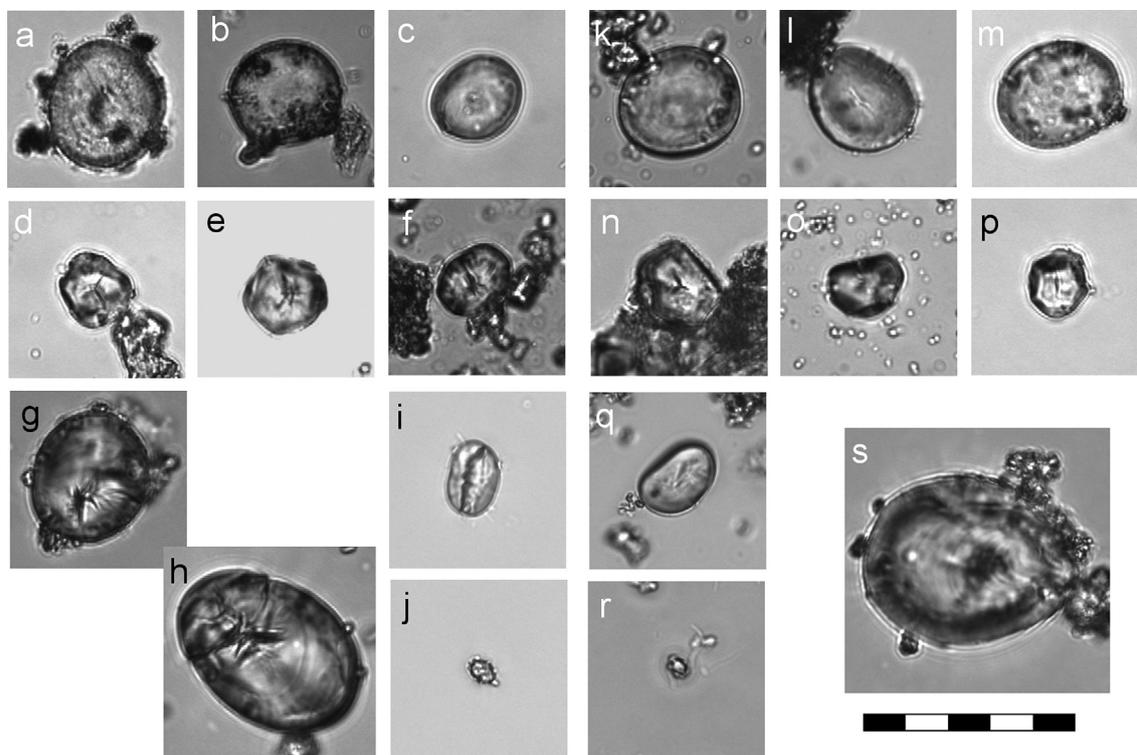


Figure 1. Archaeological plant microremains recovered from dental calculi and stone tool residues. a–j) Microremains recovered from Neanderthal samples; k–s) microremains recovered from early modern human samples. The top row are all starch grains from Triticeae seeds; the second row are starches probably from the seeds of grasses in the Andropogoneae or Paniceae tribes (AP grasses); i and q are both probable Fabeae seed starches; j and r are phytoliths from date palm (*Phoenix* spp.) fruits; g and h are starches from plant underground storage organs, likely from Nymphaeae (compare to Figure 2). a) Triticeae starch from La Quina 5 left M₃ calculus; b) Triticeae starch from La Quina stone tool number 1; c) Triticeae starch from Külna right M¹; d) AP grass starch from La Quina stone tool number 7; e) AP grass starch from Spy II tooth #5771; f) AP grass starch from Abri des Merveilles tool 13; g & h) Probable Nymphaeae starches from Spy 1 right M₁; i) Possible Fabeae starch from Shanidar III tooth 4; j) *Phoenix* fruit phytolith from Shanidar III tooth 3; k) Triticeae starch from Shanidar tool 48; l) Triticeae starch from Skhul tool 9; m) Triticeae starch from Klasies River layer 10 tool 1; n) AP grass starch from Abri des Merveilles tool 1; o) AP grass starch from Blombos tooth 8971; p) AP grass starch from Ishango 24; q) possible Fabeae starch from Shanidar tool 9; r) *Phoenix* phytolith from Skhul tool 1; s) possible USO starch from Abri Pataud left M². Scale bar is 50 μ m.

that tool or tooth never came in contact with plant matter (evidence of absence), or rather an indication that the microfossils were removed or destroyed after being deposited (absence of evidence). We believe the latter interpretation to be more conservative, and have therefore not included any of the zero values in our quantitative analyses.

Results

We recovered microremains from many but not all of the samples, and identified several types to plant taxon or plant organ (Table 1). The preservation of microremains does not appear to have been significantly affected by non-dietary processes. Across all samples, there is no correlation between geological age and microremain numbers (SOM Fig. 1; $r^2 = 0.02$; $p = 0.41$). Among teeth, there was no correlation between the weight of calculus removed and the number of recovered microremains (though not all samples were weighed) (SOM Fig. 2; $r^2 = 0.04$; $p = 0.23$). There was also no correlation between microremain numbers and formal tool classification (SOM Fig. 3; Kruskal–Wallis $p = 0.20$). With a few exceptions (see Shanidar and Skhul, below), phytoliths were very rare in comparison with starch grains. The general paucity of phytoliths strongly suggests there has been no contamination from burial sediments, since phytoliths are much more prevalent in sediments than are starches (SOM Text). The overall lack of phytoliths also suggests that the starch grains come from primary consumption of plant material rather than consumption of chyme (as suggested by Buck and Stringer, 2014) since most large bodied terrestrial herbivores consume large

quantities of phytolith-rich grasses. Other potential sources of contamination were assessed but are unlikely to have affected the assemblage (SOM Text). Many of the starches showed damage that we attribute to aging, including margin cracking and localized loss of birefringence. Some showed evidence of cooking, including partial gelatinization (Henry et al., 2009), while still others had hilum cracks and other features evocative of grinding (Babot, 2003). In most of these latter cases we have not been able to identify the species that produced the starch, and because processing damage varies between species, we have taken the conservative approach of not assigning this damage as due to grinding (SOM Text).

Results by site

The Neanderthal samples came from sites across Europe and the Near East. The calculi from Spy have remarkable microremain preservation despite being the northernmost samples (50°28'21"N, 4°40'50"E), where hunter–gatherer plant use is expected to be low (Kelly, 1995). One-third of the starches in this population were of a single type, which is from a USO of the Nymphaeae (waterlily) family (Henry et al., 2011, Fig. 1d, e, Fig. 2). A few of the starches had characteristics similar to grass seeds in the Andropogoneae or Paniceae tribes (AP grasses).¹ Several of the other recovered

¹ These grass tribes are rare but present in northern temperate areas (Cross, 1980). Though we found similar starches in a large number of our samples, we have not been able to narrow down the identification to species.

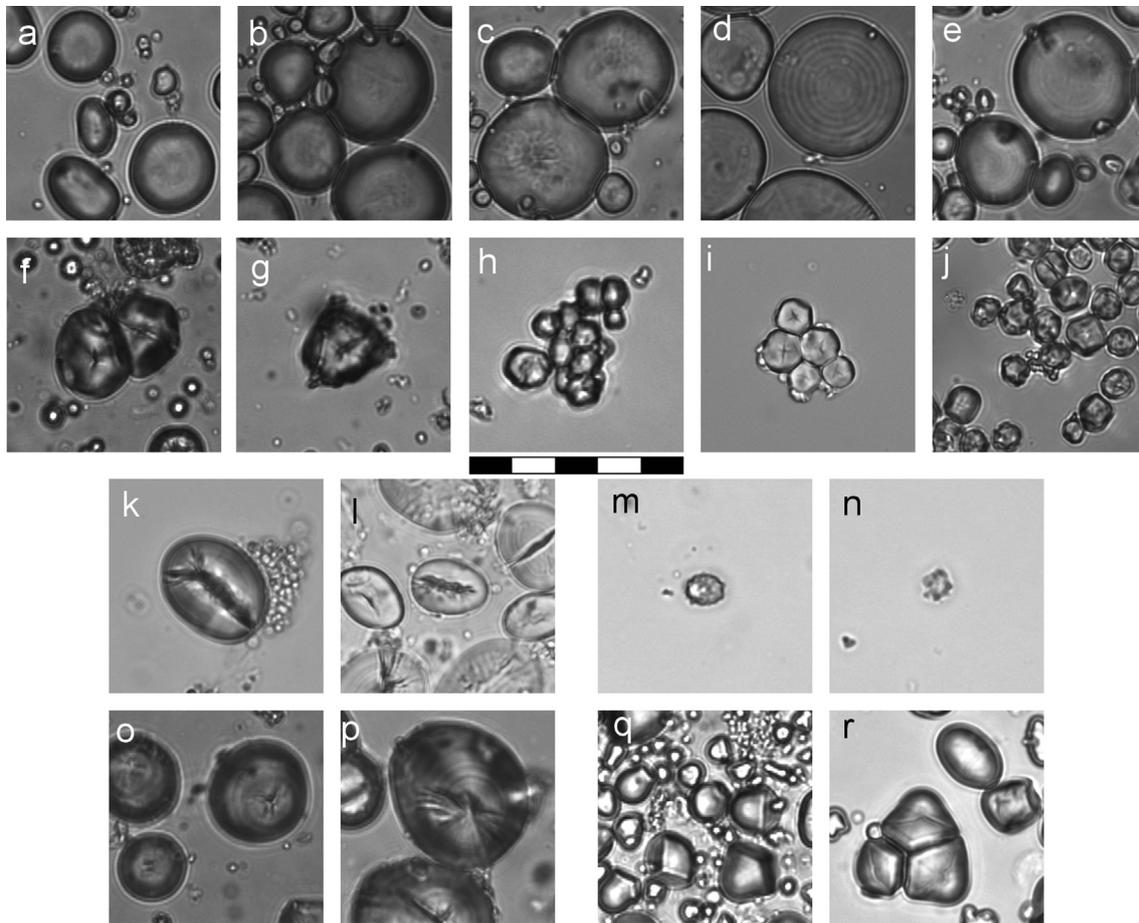


Figure 2. Starch grains and phytoliths from modern reference material. a–e) Starches from seeds of Triticeae grasses; f–j) Starch grains from seeds of grasses in the Andropogoneae and Paniceae tribes (AP grasses); k & l) starch grains from seeds from Fabaceae plants; m & n) phytoliths from fruits of date palms (*Phoenix* spp.); o & p) starch grains from underground storage organs of Nymphaeae water lilies; q & r) starch grains from underground storage organs of South African Iridaceae plants. a) *Hordeum bulbosum*; b) *Aegilops speltoides*; c) *Triticum turgidum*; d) *Aegilops longissima*; e) *Secale vavilovii*; f) *Sorghum bicolor*; g) *Sorghum halepense*; h) *Brachiaria dura*; i) *Setaria italica*; j) *Panicum miliaceum*; k) *Pisum sativum*; l) *Cicer arietinum*; m) *Phoenix dactylifera*; n) *Phoenix reclinata*; o) *Nymphaea alba*; p) *Nuphar lutea*; q) *Sparaxis bulbifera*; r) *Babiana cedarbergensis*. Scale bar is 50 μ m.

starches could be categorized into four other unknown types, but the majority of starches from the Spy samples either was diagnostic-looking but not represented in the reference collection, or were too damaged or encrusted to confidently assign to one of the types (SOM Table 2; SOM Fig. 4). We found fewer microremains in the other European Neanderthal calculi (Arcy-sur-Cure, Goyet, Kůlna, La Chapelle-aux-Saints, La Ferrassie, La Quina, Malarnaud and Montmaurin), though these came from several, yet unidentified, plant types (SOM Tables 3 and 4; SOM Fig. 5). One-quarter of the starches from the Kůlna calculus are from grass seeds in the Triticeae tribe, which includes the wild relatives of wheat and barley (Fig. 1; SOM Text; SOM Table 4; SOM Fig. 6). The stone tools from La Quina preserved a large number and variety of microremains, including several from the Triticeae (Fig. 1; Table 1; SOM Table 5; SOM Fig. 7). Several of the starches from the La Quina tools also were damaged in a manner evocative of processing (SOM Text). Though the preservation varies, there are two important similarities among the Neanderthal samples. Seeds from Triticeae and possibly other grass tribes were a common resource, and a variety of other plant types including USOs were also consumed.

Some of our sites had both Neanderthal and modern human populations, which allowed direct comparisons of their behaviors in similar environments. Shanidar Cave had three populations: one represented by the calculi from the Shanidar III Neanderthal, another by stone tools from the Middle Paleolithic Mousterian level

(‘D’), and the last by stone tools from the Upper Paleolithic Baradostian level (‘C’). The Shanidar III calculi were the most productive samples, preserving starches from Triticeae grass seeds, a probable legume starch (subfamily Faboideae and possibly tribe Fabaeae), another likely from a USO, phytoliths from date palms (*Phoenix* spp.), and several other probable tree fruit phytoliths (Henry et al., 2011, Figs. 1 and 2; SOM Table 6; SOM Fig. 8). The large number and diagnostic features of the Triticeae starches enabled us to identify them as deriving from *Hordeum* spp. (wild relatives of barley), and several showed clear evidence of cooking (Henry et al., 2011). The stone tools from both levels also preserved Triticeae starches, date palm phytoliths, and a variety of other starch types (Fig. 2; SOM Table 7; SOM Fig. 9), though none presented cooking damage. Although more tools from the MP layer were sampled, more microremains and two extra starch types were recovered from the UP tools (SOM Table 7: Type 8). This could indicate a slight dietary change between the MP and the UP groups, particularly as the UP tools had the highest Menhinick’s index in this study (5.24), while the MP tools have a lower value (3.55). However, all of the samples from Shanidar, including the teeth, have some of the highest Menhinick’s values in this study, and the calculus values fall between the two tool populations (4.77), suggesting that this difference is actually quite small. Furthermore, the identified microremain types from the UP tools, including the Triticeae starches and a possible Fabaeae seed starch (Fig. 2k), are identical to those starch

types recovered from the MP tools and the Neanderthal dental calculus. These overlapping types suggest that many of the same plant foods were consumed during the MP and UP at Shanidar.

Two other sites, Abri des Merveilles and Gorham's Cave, also had both Middle and Upper Paleolithic populations. Though these stone tools did not preserve an abundance of microremains, the assemblages appeared to have similar microremain types. The two assemblages from Abri des Merveilles have representatives of two different kinds of Triticeae starches, and some likely AP grass starches (Table 1; SOM Table 8; SOM Fig. 10). The MP tools had several starches belonging to a type not seen on the UP tools (SOM Table 8; Type 4), but there were more damaged and unique grains on the UP tools, which accounts for the slightly higher Menhinick's index for the UP tools. At Gorham's Cave, both the MP and UP layers had Triticeae and AP grass seed starches, and two other common types that are yet unidentified (SOM Table 9; SOM Fig. 11). A unique starch from the UP sample was likely from a USO. Overall there appear to be few consistent differences between Neanderthal and modern human populations from the same sites.

The modern human populations included both early, Middle Paleolithic and Middle Stone Age (MP/MSA), and later, Upper Paleolithic and Later Stone Age populations (UP/LSA). The MP/MSA populations come from Africa and the Near East. All six of the South African populations (four from Klasies River and two from Blombos) come from the later part of the MSA and from similar localities in the Fynbos environment.² There are few differences among these assemblages. All contain starches from grasses, though at Klasies both Triticeae and AP grasses are seen, while the Blombos teeth have only AP grasses (SOM Tables 10–12; SOM Figs. 12–14). One unidentified species was found on both the Klasies tools (Type 3) and Blombos teeth (Type 2), suggesting dietary overlap between these groups. All of the Triticeae type starches from the Klasies teeth display considerable damage (SOM Fig. 12), though this damage is not seen on the tools. A variety of other, yet-unidentified starch types were found, though these were in low numbers, and they did not appear in all of the assemblages. Though it has been proposed that USOs from the Iridaceae family were dietary staples for humans living in the coastal Fynbos environment (Deacon, 1993), we found no evidence among the South African samples for consumption of these plants, despite having abundant South African representatives of this family in our reference collection. None of the Blombos samples recorded any evidence of USO use, and though several starches from the Klasies River calculi appear to be USOs, they can only provisionally be assigned to this plant part.

The MP modern human populations are represented by the samples from Skhul Cave. The calculi from several individuals preserved only moderate numbers of microremains, though there was one date palm phytolith and a few probable Triticeae starches, as well as damaged starches that suggested cooking and processing (Fig. 1; SOM Table 13; SOM Fig. 15). The stone tools were much richer in microremains, and many more types were represented, including Triticeae seed starches, date palm phytoliths, and probable AP grass seed starches (SOM Table 14; SOM Fig. 16). While some of the starches were damaged, this was not consistent with cooking damage. One recovered starch was very similar to Type 7 from the Shanidar tools.

A comparison among the MP/MSA modern human populations at Skhul, Klasies, and Blombos suggests that these groups consumed similar numbers of plant types, including a variety of grass seed starches. With the exception of the tools from Skhul, the

Menhinick's indices for these populations are all in the mid range, around 2. The Skhul tools may be something of an outlier, more similar to the other Near Eastern samples from Shanidar. Among the MP/MSA modern human samples, the majority of types differ morphologically and thus represent the consumption of quite different species among these populations, as expected for sites so geographically separated.

The later, UP/LSA modern human populations are from Europe and Africa. Those from Europe (Abri Pataud, La Madeleine, Cro Magnon, and Předmostí) did not preserve a large number of microfossils, though several types were represented (Table 1; SOM Table 15; SOM Fig. 17). None matched those from Triticeae or AP grass seed starches, but one of the Abri Pataud starches appears quite similar in size, shape, and diagnostic features to the probable Nymphaeaceae starches from Spy (Fig. 1s). The calculus samples from the LSA population at Ishango are the youngest in this study. Though the microremain preservation was not very high, the calculus from both the older and younger periods contained starches that were likely from the seeds of Triticeae and AP grasses, but the older individuals (15, 16 and 24) additionally preserved several very unique though yet unidentified starches, some of which may represent USOs (SOM Table 16; SOM Fig. 18). Unsurprisingly, with this level of microfossil preservation, the Menhinick's indices of these populations are low, below 2.

Results of the GLMM

The two GLMMs were designed to test the effect of species allocation, geographical area, and associated technology on the number of microfossil types found on a sample. We plotted the number of microfossil types recovered from each sample for teeth and for tools against species and geographic area. A visual inspection of the data suggests that there may in fact be an effect of these predictors (Fig. 3). However, the full GLMMs also account for the influence of random factors (site and individual), for the number of microfossils recovered, and for the age of the sample. Neither the full model for the tools nor that for the teeth were significantly different from their respective null models (Table 2 (p value tools = 0.38, p value teeth = 0.23)), indicating that none of the predictors we included in the models (species, geographical region, tool technology) strongly influence the number of microfossils recovered on the teeth and tools examined here.

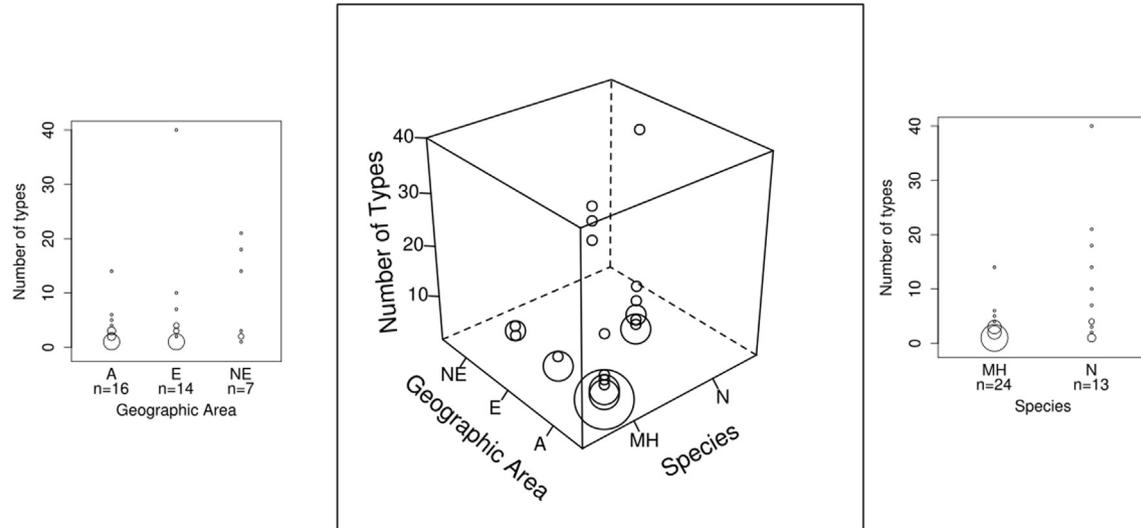
Tests of predictions

We proposed that, if Neanderthals' consumption of plant food followed previous views and interpretations, then we should find fewer plant types and less evidence for 'costly' plant foods in Neanderthal assemblages than in early modern human ones. The results indicate that we must reject these hypotheses. Almost every population in this study had starches from grass seeds and/or USOs (Table 1). Both Neanderthals and modern humans consumed these potentially costly resources, though grasses and USOs were slightly more common in modern human populations. The GLMMs indicated that there was no strong effect of species, Neanderthal or modern human, on the number of plants recovered from a sample, indicating that neither group consumed more plant types than the other.

We also explored whether associated stone tool technology and geographic region influenced plant food consumption. The GLMMs suggest that neither for teeth nor for tools is there an apparent increase in the number of plants consumed in later, UP/LSA populations. There is also no discernible effect of geographic region on microfossil types. We expect that this may be a result of the very coarse geographic divisions considered here. There are many

² The excavators of Klasies River suggest that the samples from Cave 1 Layer 14 and Shelter 1b layer 10 represent the same occupation of the site (Singer and Wymer, 1982).

Number of microremain types recovered from calculus samples



Number of microremain types recovered from tools

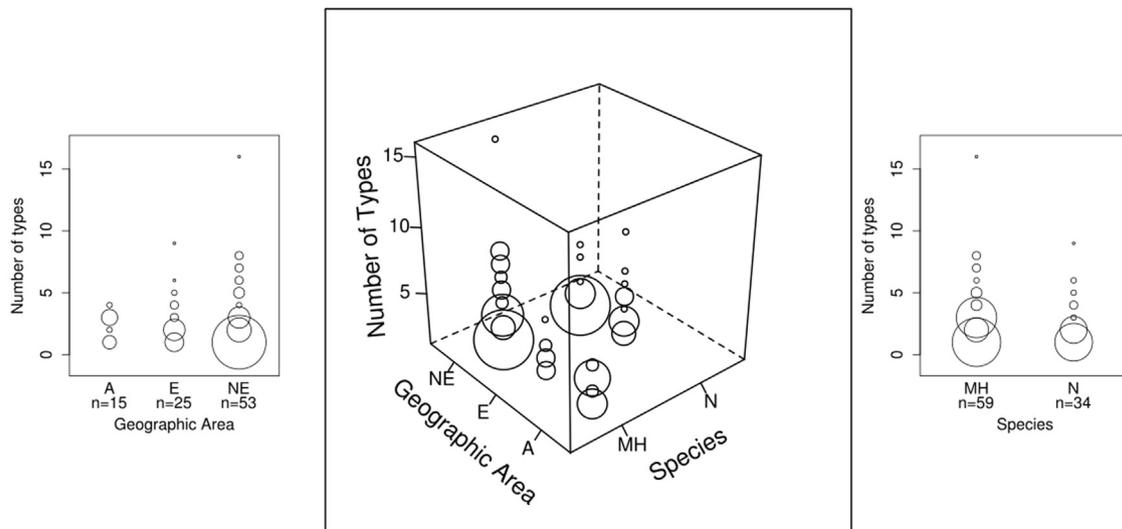


Figure 3. Comparisons of dietary breadth among the populations considered in this study. The top row are counts of microremain types per calculus sample, grouped by species on the right and geographic region on the left, and both simultaneously in the middle. The bottom row shows the same comparisons for tool samples. The size of the circle represents the number of samples that share the same number of types, but the scaling factor for circle size differs between the central plots and the edge plots. N = Neanderthal, MH = modern human, NE = Near East, E = Europe, A = Africa. While the edge plots suggest that there may be differences between species or between areas when considered alone, the center plots clearly indicate that when both species and area are considered together, there is no consistent pattern of variation. There is a similar result when comparing species and associated tool technology and geographic region and associated tool technology.

environments subsumed within both our European and African samples (as has been considered by [El Zaatari et al., 2011](#); [Fiorenza et al., 2011](#)), and their effect on plant diet may be masked by lumping them together. Future studies including more sites and finer ecogeographic divisions may reveal these patterns.

Discussion

Our results indicate that Middle Paleolithic Neanderthals probably consumed as many plant species as modern humans did. This lack of evidence for a shift in diet breadth between Neanderthals and modern humans contrasts with the results from studies of animal foods (e.g., [Stiner et al., 2000](#); [Richards and Trinkaus, 2009](#)). The generation of a sizable amount of data on plant exploitation from the microremains records suggests a more complex picture of

Neanderthal and modern human dietary behavior than previously drawn. We propose that Neanderthals' routine and varied use of plant foods reflects an investment in technology and division of labor.

Neanderthal tool assemblages lack certain formal types, particularly complex projectiles and fishing implements, that are more common in modern human assemblages ([Brooks et al., 2006](#); [d'Errico and Henshilwood, 2007](#); [Shea and Sisk, 2010](#)). These tools decrease the immediate cost of procuring fast, dangerous, or otherwise low-ranked game ([Bird and O'Connell, 2006](#)). However, the development and curation of these complex tools is also costly, so should only be undertaken when overall foraging efficiency is reduced due to increased processing costs of preferred foods ([Bird and O'Connell, 2006](#)). In contrast to capturing small fast animals, plant collecting and processing does not require complex

Table 2

a) Test of the glmm for tools. b) Test of the glmm for calculus.

	DF	AIC	BIC	log Lik	Chisq	Chi df	P
a)							
tnull	4	113.59	123.72	−52.797			
tres	13	121.95	154.88	−47.977	9.6414	9	0.3803
b)							
cnull	4	104.17	110.5	−48.084			
cres	8	106.63	119.3	−45.315	5.5385	4	0.2364

tnull: number of microremain types ~ average age of the site + (1 | site) + (0 + number of microremains | site).

tres: number of microremain types ~ species + geographic area + associated tool technology + tool type + (1 | site) + (0 + number of microremains | site).

cnull: number of microremains ~ average age of the site + (1 | individual) + (0 + number of microremains | individual).

cres: number of microremains ~ species + geographic area + associated technology + average age of the site + (1 | individual) + (0 + number of microremains | individual).

technology to procure a wide variety of plant foods. A digging stick and a method for boiling or roasting are sufficient for many plant foods (Lee, 1979; Marlowe, 2010).

Certain resources like grass seeds and nuts require some amount of processing, including shelling or grinding, but it can be performed without the use of complex technology. Many grass seeds and nuts can be mass-collected in a way that increases their relative ranking (Masden and Schmitt, 1998), for example, by beating stands of grass seeds into a container (Wilke et al., 1972), by raiding insect caches (see Bohrer, 1991), or by hand-harvesting in dense patches (Harlan, 1967). The lack of formal grindstones at most Neanderthal sites should not necessarily be interpreted to mean that this simple plant processing technology did not exist. Grinding, pounding, or shelling could have been done using tools that are either not preserved in the archaeological record, such as wooden implements, or not recognized as plant processing implements, such as bedrock grinding surfaces (Gorecki et al., 1997) or other unmodified stones (Zarrillo and Kooyman, 2006). Furthermore, if the processing of plants by grinding was only an occasional dietary behavior, there should be little investment in formal grinding tools (Bright et al., 2002). Studies of modern foragers have shown that individuals should process some amount of plant foods in the field as part of a trade off between processing and transportation (Metcalfe and Barlow, 1992). These 'off-site' processing areas would likely be missed in most archaeological surveys (Brooks and Yellen, 1987). The cooked starches in the Neanderthal assemblage indicate that they did use some simple processing methods.

It is possible that with the technologies the Neanderthals had in hand, certain plant foods would have been more highly-ranked than small, fast, and hard-to-catch animals (Stiner and Kuhn, 1992; Stiner et al., 1999, 2000) because the plants were accessible without the development and curation of new tools (Bright et al., 2002; Bird and O'Connell, 2006). At low population densities, large mammals and a broad plant diet probably would have been sufficient to meet the dietary needs of Neanderthals (O'Connell, 2006; Hockett, 2012). Where external pressures such as environmental changes or competition with early modern humans would have promoted increased dietary breadth, it may have been easier for Neanderthals to rely more heavily on the section of diet for which they already had an established expertise rather than to engage in the potentially risky development of different and more complex hunting technologies.

Another aspect of Neanderthal behavior suggested by our results is that there may have been some kind of division of labor within Neanderthal groups. Some have interpreted Neanderthals'

focus on large game and the lack of evidence for their use of plant foods to be consistent with both men and women hunting large game (Kuhn and Stiner, 2006; Stiner and Kuhn, 2009). Our data indicate that some individuals within Neanderthal society collected a variety of plant foods. The richness of the plant diet at many of the Neanderthal sites strongly suggests a level of specialization in gathering, as would be expected if a subset of the Neanderthal society regularly gathered plants and another did not. There is no guarantee that gathering was done by women. Older individuals or other, socially-defined subsets could also be the primary gatherers, but it is reasonable to suggest from these data that Neanderthals had a social structure oriented toward dividing labor for resource pursuits.

Conclusion

This picture of Neanderthals subsistence as oriented toward routinely pursuing big game and collecting plants is still compatible with the idea that the overall diet and more sophisticated toolkit of modern humans gave them a competitive advantage as they moved into the Near East and Europe. When early modern humans moved into Neanderthal areas and were directly competing with them for food, Neanderthals probably had several options that enabled them to obtain more calories. They could copy the technology and dietary habits of modern humans, or further increase their use of plant foods. Some authors argue that later Neanderthals did adopt modern human technologies (Mellars, 1999), but analogues to modern foragers suggest there may have been strong social costs for Neanderthals who tried to join or emulate modern human groups (O'Connell, 2006), which would make the adoption of modern human behavior or technology less adaptive than maintaining a traditional lifestyle. A second option is to retain a traditional diet but increase the proportion of lower-ranked foods. It is possible that Neanderthals underwent dietary stress due to competition with early modern humans, and they may have responded in part by consuming more plant foods. There is probably a limit to how well plant foods can compensate for a reduction of large game if smaller, faster-moving game are not exploited, particularly given Neanderthals' high energy needs (Aiello and Wheeler, 2003; Froehle and Churchill, 2009). This lack of dietary flexibility due to technological and social constraints may have contributed significantly to the extinction of Neanderthals, even if a lack of plant foods in the diet did not.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at <http://dx.doi.org/10.1016/j.jhevol.2013.12.014>.

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