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Did the moderns kill off the Neanderthals? A reply to F. d'Errico and Sánchez Goñi ☆

1. Introduction

In a recent paper d'Errico and Sánchez Goñi (2003) draw a distinction between climate and human action as mutually exclusive potential causes of the extinction of the Neanderthals. They come to the conclusion that, because in their view climate cannot be demonstrated to have caused the Neanderthal extinction, by default it must have been caused by the arrival of the Moderns. In their paper d'Errico and Sánchez Goñi go as far as to state that "it is clear that the *coup de grace* to the last Neanderthals was given by competition with Moderns colonising the South of the peninsula (Iberia) after the H4 event." We disagree with this view and, as some of us have done previously (see Balter, 2001), we challenge students of the Neanderthal extinction to provide direct evidence of competition from Modern Humans on Neanderthals. To date no such evidence has been put forward. In this paper we remind d'Errico and Sánchez Goñi (2003) and other claimants of Modern competitive exclusion over Neanderthals of the basic principles of ecology that they must first satisfy.

2. Competition

In considering competition, a knowledge of the nature of the participants that we are dealing with is desirable. In other words were Moderns and Neanderthals different species (Stringer, 2002; Tattersall, 2002) or were they a single species (Hawks et al., 2000; Wolpoff and Caspari, 2000)? This would lead us to study inter- or intra-specific competition respectively. This problem has no immediate resolution as we are unable to apply the biological species concept to fossils (Cain, 1971; Finlayson, 2004). We consider that the safest way to proceed on available evidence is to consider all members of the genus *Homo* at any particular point in time to form a polytypic species (Aguirre, 1994). This, in some way, permits us to consider Moderns and Neanderthals as contemporary populations that could have responded to each other's presence in a mosaic of ways with multiple outcomes that would have depended on ecological circumstances and historical contingency.

Competition is effective in structuring communities when these are at equilibrium. On the other hand, it is of less importance in situations where there are wide environmental fluctuations and there is unpredictable disturbance (Wang et al., 2002). The reason for this is that such populations are constantly moving towards situations of carrying capacity but are regularly pegged back by unfavourable conditions. d'Errico and Sánchez Goñi (2003) very ably demonstrate that the conditions during OIS 3 were highly variable, something that not only applies to Iberia but to much of Eurasia and Africa (Finlayson, 2003). A sound explanation has to be given by advocates of competition that explains their claimed "special" case in the history of the planet—that of competition driving a world population to extinction in conditions of high environmental fluctuation where it has not even been remotely shown that these populations were at carrying capacity. We remind those advocates of competition that current evidence strongly indicates a pattern of sparse, low-density, human dispersion in Eurasia throughout the Pleistocene (Harpending et al., 1998; Richards et al., 1998; Rolland, 1998).

We also reflect on those instances of apparent coexistence of distinct ecological populations in different parts of the world, including Neanderthals and Modern Humans, over protracted periods in the Pleistocene without any indication of competitive exclusion of one population over another (Soffer, 1994; Bar-Yosef, 1994, 1998; Van Peer, 1998). In all such cases the populations are living in areas of high environmental heterogeneity (Finlayson, 2004) and the observations are in keeping with ecological theory that predicts long-term coexistence of very similar species in areas of environmental heterogeneity (Hanski, 1983; Taneyhill, 2000). Since Iberia is a particularly environmentally heterogeneous peninsula (Finlayson et al., 2000) claimants of competition in Iberia have to explain why and how their models deviate from theoretical expectation.

For the moment we retain the view previously expressed (Finlayson et al., 2000) that, if competition between Moderns and Neanderthals ever took place at all, it would have been ephemeral and would not have determined the final outcome of the two world populations. Paradoxically, we expect that if regional and local

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competition ever took place between Moderns and Neanderthals it should have favoured the Neanderthals. The reason for this expectation is that in a situation of an expanding population (Moderns) and a stable one (the Neanderthals), the resident population would be expected to have the competitive edge over the pioneers because of their superior local knowledge of territory characteristics, available resources and optimal methods of resource collection. Proponents of superior Modern competitive ability have to concede that our perspective is at least as valid as theirs and that it is enormously difficult to disentangle the two views on the basis of the available evidence—that of Aurignacian (Modern) levels always appearing above Mousterian (Neanderthal) levels in archaeological sites. In our view it is presumptuous to interpret such evidence in favour of Moderns ousting Neanderthals when it can be equally cited as evidence of Moderns only being able to occupy such sites once Neanderthals have gone.

3. The role of climate

d'Errico and Sánchez Goñi (2003) correctly state that the archaeological and anthropological records for the transition are ambiguous. They then proceed to treat this same record and match it to the finer resolution of their marine cores. It is precisely because of the ambiguity of the record of human occupation that we have consistently (Finlayson et al., 2000; Finlayson, 2003, 2004; Giles Pacheco et al., 2003) argued that the best that we can do on present evidence is attempt to understand the large-scale processes that affected the dynamics of the various human populations that inhabited Eurasia. There is some degree of certainty and agreement that the Neanderthals became extinct towards the end of OIS 3. This is also the time when the Moderns (taken as the arrival of people with Aurignacian technology) spread across Europe, from east to west (Otte, 1994; Semino et al., 2000; Bosch et al., 2001; Wells et al., 2001). The spread of the Aurignacians into Iberia appears slow and sporadic, there being little evidence of a presence in the extreme south (Giles Pacheco et al., 2003). We lack the precision today that allows us to time the exact arrival of the Aurignacians and the extinction of the various last Neanderthal populations anywhere. The last dates available for Mousterian technology do not represent the last Neanderthals—they represent Neanderthal populations that were present at sufficiently high numbers for them to be detected in the archaeological record. Similarly the first dates of the Aurignacians are not those of the first Aurignacians. The level of precision that d'Errico and Sánchez Goñi (2003) seek to achieve in, for example, matching human population levels (itself questionable on the evidence presented which lacks statistical treatment) with climatic events such as H4 is simplistic. Our own approach has sought to establish those features of the environment that are distinctive during OIS 3, particularly the latter part, and that may have contributed to depressing and fragmenting Neanderthal populations beyond recovery and, similarly, that may have permitted the expansion of the Aurignacians. The factors that eliminated the last Neanderthal populations will be difficult to establish. It will require detailed analysis of individual sites and we may never establish all the modes of extinction. At Gorham's Cave in Gibraltar it appears to have been habitat and resource loss (Finlayson and Giles Pacheco, 2000), but this need not have been the case in other populations. Thus modes of extinction of local Neanderthal populations may have included stochastic effects, disease, local competition, inbreeding, genetic swamping and Allee effects (Finlayson, 2004). d'Errico and Sánchez Goñi (2003), in the case of Gorham's Cave, confuse our statement regarding the stability of the environment off Gorham's Cave. Our reference (Finlayson and Giles Pacheco, 2000) dealt with mammalian herbivore composition as a food resource and to vegetation structure. The same suite of species and vegetation structure was available for much of OIS 3 and would thus have been perceived as constant by Neanderthals. Climatic fluctuations would have shifted vegetation patterns spatially and would have affected mammalian herbivore density, probably with corresponding shifts in Neanderthal ecology. It is only during the end of OIS 3 that we can detect at this site a major change in vegetation structure (towards dense montane forest) and the arrival of arctic marine vertebrates.

So are there any features of the end of OIS 3 that might provide clues as to the events that unfolded in Europe at the time? Finlayson (2003) has shown that the second half of OIS 3 was the most climatically unstable period of the Pleistocene (Fig. 1) and there is much supporting evidence that shows that environmental changes were often rapid (e.g. Allen et al., 1999). Indeed, it is an argument used by d'Errico and Sánchez Goñi (2003) themselves. We have previously suggested (Finlayson, 2003, 2004) that it is the frequency and amplitude of these fluctuations, and not necessarily their intensity, that are the key to understanding the fragmentation of the Neanderthal populations.

There are misconceptions regarding the effects of climate on ecology and human populations in d'Errico and Sánchez Goñi's (2003) paper that we must now address. First, in using site data for analysis d'Errico and Sánchez Goñi (2003) seem unaware that some sites may represent source populations and others sinks (e.g. Hanski and Gilpin, 1997). Source populations are those in which reproductive output exceeds mortality whereas sinks are maintained by immigration. Their presence could, paradoxically, be largely independent of existing environmental conditions. There may be a number of

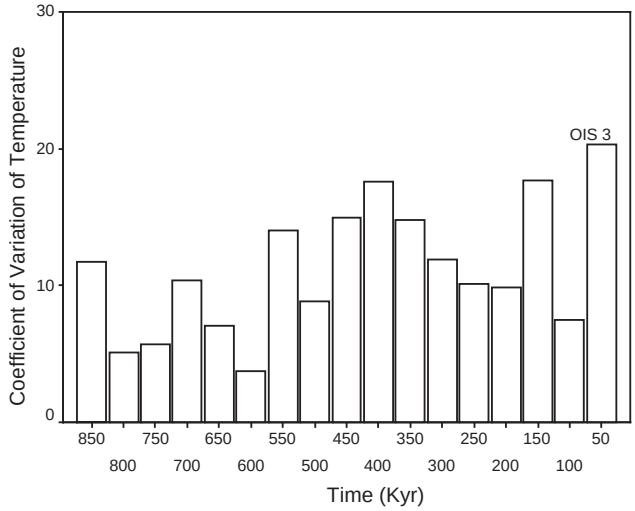

Fig. 1. Distribution of coefficient of variation of temperature during the last 850 kyr (after Finlayson, 2003).

sink populations in their analysis (that cannot be detected in the archaeological record) that are simply being maintained by immigration. Second, time lags are not recognised. d'Errico and Sánchez Goñi (2003) assume that events and their causes can be precisely matched. They ignore the cumulative effects on populations. For example, the extinction of the Neanderthals at the end of OIS 3 may be due to a series of factors that cumulatively reduced these populations to the point of no return. The last populations may have existed as "living dead", that is populations that still had a number of generations to run but, no matter how favourable events became, they would still go extinct (Gilpin and Soulé, 1986; Groom and Pascual, 1998). So the paradox of Neanderthal populations becoming extinct during favourable conditions, if that was indeed the case, is perfectly explicable from ecological theory. To claim that Neanderthals did not become extinct during a particular climatic event is irrelevant. Time lags would also have affected vegetation and faunal movements, further emphasizing the futility of attempting the precision that d'Errico and Sánchez Goñi (2003) expect.

4. What do the marine cores tell us?

The two cores used for d'Errico and Sánchez Goñi (2003) study are insufficient to resolve the complex ecological history of southern Iberia with its small-scale mosaics. In the first place, their suggestion that the pollen assemblages reflect regional changes of importance is not substantiated but remains an act of faith. The reality is that d'Errico and Sánchez Goñi (2003) do not know the area that their marine core is sampling and, therefore, the extent to which it is indeed representative of conditions in southern Iberia. The inconsistencies that they observe in other records (terrestrial pollen, anthracological, etc.) are explained away in multiple ways. Their dismissal of the inconsistencies between their core and that of Padul, without real scientific reasons, exemplifies their approach. d'Errico and Sánchez Goñi (2003) seem unaware of the significance of the location of their core MD95-2043, between the arid lands of Granada and Almería in the north and the North African arid lands in the south (Fig. 2). It is only natural to expect that their pollen is derived mainly from these zones that, even today, are distinctively arid and very different from areas immediately to the west and north. So to conclude that the whole of southern Iberia was arid during a particular moment in the Pleistocene, as they do, is invalid. Similarly, their Portuguese core MD95-2042 is far removed from the thermo-Mediterranean bioclimates further south and is presumably largely sampling meso-Mediterranean bioclimates to the east. The whole point about southern Iberia is that it is an ecological mosaic at small scales and it is this small-scale mosaic that made it a major European refugium for plants and animals (Carrión et al., 2000; Hewitt, 1996, 1999, 2000). Had it been subjected to the blanket episodes of cold and aridity that d'Errico and Sánchez Goñi (2003) would have us believe then much of the Mediterranean fauna and flora that exists today would have gone. Their assertion that two pollen cores, one off Portugal and the other in the Alborán Sea, provide a detailed picture of the climatic and vegetational changes of southern Iberia is therefore unsubstantiated as are their generalised

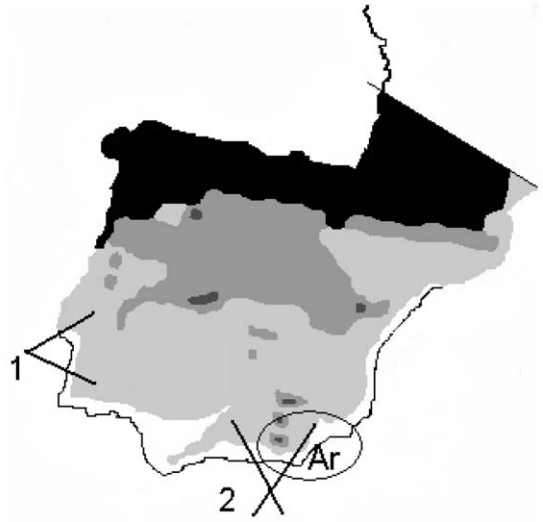

Fig. 2. Location of d'Errico and Sánchez Goñi's (2003) marine cores in relation to current bioclimates of Iberia. 1—core MD95-2042; 2—core MD95-2043; Ar—approximate area of arid lands in south-eastern Iberia. Bioclimates after Rivas-Martínez (1987); black—Eurosiberian; dark grey—Oro/Crioro-Mediterranean; intermediate grey—Supra Mediterranean; pale grey—Meso-Mediterranean; white—Thermo-Mediterranean.

vegetation descriptions. d'Errico and Sánchez Goñi's (2003) attempt to begin to understand southern Iberian palaeoecology from detailed marine cores is nevertheless laudable and further cores, if they become available, will undoubtedly aid our understanding.

5. Understanding Iberian ecology

d'Errico and Sánchez Goñi (2003) write as though the formula: wet + humid = good for humans, cold + arid = bad for humans, explains Iberian events. This is a misconception. For a start the forestation of southern Iberia during warm and humid periods was, in all probability, unfavourable for humans. We have insufficient evidence for the Neanderthals but it is easily demonstrable in the late Upper Palaeolithic. The expansion of the forests may have been an important contributory factor to the decrease in human populations in the south during the Magdalenian (Giles Pacheco et al., 2003; Finlayson, 2004) when most populations were concentrated on the coasts and lived off marine resources. Forests are too dense for effective hunting and were largely unused by humans for much of the Pleistocene (Gamble, 1993; Finlayson, 2004). We suspect a similar pattern of human response in all interglacials but must await further evidence to verify this point. Intermediate climates between interglacials and glacials would have provided a mosaic of ecotonal environments, such as those off Gorham's Cave in Gibraltar (Finlayson and Giles Pacheco, 2000), that were exploited by the Neanderthals. Cold and arid events were not necessarily unsuitable, especially for the Aurignacians that had the mobility strategies to deal with such environments (Finlayson, 2004). There is a generalised misunderstanding that sandy areas are ecologically unsuitable. In fact they can be remarkably rich and hold large mammalian herbivore resources (Finlayson and Giles Pacheco, 2000). d'Errico and Sánchez Goñi's (2003) ecological arguments are therefore also invalidated.

6. So who killed the Neanderthals?

d'Errico and Sánchez Goñi's (2003) paper is useful in that it reinforces the data that show that climatic events worldwide became increasingly unstable during OIS 3. It is probably no coincidence that this instability, the Neanderthal extinction, and probably that of other large mammals, occurred at about the same time. In that sense their paper reinforces the view that the Neanderthal populations were heavily influenced in a negative way by intense climatic instability. Their data are also indicative of a relationship between cold and arid events and the penetration of Iberia by Modern Humans. Where they exceed the limits of their data is in coming to the conclusion that the two human events, apparently moving in opposite directions, are cause and effect. We suggest that this is a spurious correlation and that what are being observed are two populations responding to the same variable (or variables) in opposite directions. Since no direct proof of cause and effect between Aurignacians and Neanderthals is advanced, this must remain the most parsimonious explanation. Finally, d'Errico and Sánchez Goñi (2003) repeat the criticism that if Neanderthals had been affected by climate, they should have gone extinct during similar events earlier. We have explained this point previously (Finlayson et al., 2000; Finlayson, 2004) but will repeat it here once again. It is naïve to expect that there will be equal, even similar, responses of populations to similar events because we are dealing with history and not with controlled scientific experiments. Since we do not know the starting template in each event we cannot predict the outcome. Thus, two equal climatic events could cause a population decrease in one and an extinction in the other if, simply, starting population sizes were very different. In conclusion, the evidence available to us increasingly points to climate instability fragmenting Neanderthal populations and d'Errico and Sánchez Goñi's (2003) paper, ironically, supports this position. We cannot determine smaller-scale modes of extinction of the fragmented populations. Indeed, we do not even know when these became extinct. Finally, there is not a single piece of evidence currently available that conclusively demonstrates a competitive effect of Moderns on Neanderthals anywhere in the planet. That is the real challenge that faces proponents of active Neanderthal replacement by Modern Humans.

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