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Bio-cultural interactions and demography during the Middle to Upper Palaeolithic transition in Iberia: An agent-based modelling approach

Carolina Cucart-Mora [a, b, *], Sergi Lozano [a, b], Javier Fernández-López de Pablo [a, b]

[a] Institut Català de Paleoecologia Human i Evolució Social (IPHES), Campus Sescelades, Edifici W3, Tarragona, Spain
[b] Àrea de Prehistòria, Universitat Rovira i Virgili, Avda. Catalunya 35, Tarragona, Spain

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ABSTRACT

The Middle to Upper Palaeolithic transition was a process of cultural and biological replacement, considered a turning point in human evolutionary history. Various hypotheses have been used to explain the disappearance of Neanderthals from Eurasia. However, very few studies have explicitly examined the causative role of demography on Neanderthal and anatomically modern humans (AMH) interaction. Here we use an integrative method based on computational modelling and the analysis of archaeological data to construct an agent based model that explores the influence of demographic variables (birth and death rates) and mobility (home range size) on the bio-cultural interaction between AMH and Neanderthals during the transition from the Middle to Upper Palaeolithic on the Iberian Peninsula (50 ka to 30 ka BP). Our simulation results are consistent with the current radiocarbon framework for the disappearance of Neanderthals in this region. This suggest that the extinction of Neanderthals could be explained by inter-specific differences in demographic behaviour and mobility patterns compared with AMH.

1. Introduction

The Middle to Upper Palaeolithic transition, ranging from 50 ka to 30 ka BP, was a process of cultural and biological replacement considered a turning point in human evolutionary history. As anatomically modern humans (AMH) expanded from the Levant into Europe, they encountered, and biologically interacted with, the pre-existing Neanderthal populations, causing their disappearance from the palaeo-anthropological record.

Various hypotheses have been used to explain the disappearance of Neanderthals from Eurasia. Some scholars have suggested that the extinction of Neanderthals was related to the arrival of AMH, -given their more complex cognitive abilities; their inventiveness and capacity for innovation (Klein, 2008; Mellars, 2005); complex symbolic and linguistic behaviour (Conard, 2003; Zubrow, 1989); exploitation of a broader range of resources (Stiner and Munro, 2002); planning capacity, including larger-scale social networks (Nash et al., 2013); sexual division of labour (Kuhn and Stiner, 2006) and larger population sizes-(Bocquet-Appel et al., 2005; Mellars and French, 2011). In contrast Zilhão (2006) and D'Errico and Stringer (2011), among others, hold that innovations indicative of the modern condition were not exclusive to AMH, but they appeared and disappeared several times in Africa and Eurasia between 200 and 40 ka, at which point they became fully consolidated (McBrearty and Brooks, 2000). The Neanderthal archaeological record has also provided evidence for the consumption and exploitation of small prey, lagomorphs, avifauna and marine resources(Blasco et al., 2015; Finlayson et al., 2012; Fiore et al., 2014; Hardy et al., 2013; Zilhão, 2007) in addition to other modern features (Villa and Roebroeks, 2014). Other researchers suggest that there is a connection between population growth and the emergence and fixation of modern behaviour (Premo and Kuhn, 2010; French, 2016). On the other hand, Collard et al. (2016) suggest that such a relation has not yet been proven, therefore, it should be treated as one (not the only/unique/main) of the many explanatory factors for the emergence of modernity.

Since the publication of the first draft sequence of the Neanderthal genome (Green et al., 2010) the debate on the demise of Neanderthals must be framed in terms of some degree of interbreeding. Significant efforts have been invested in determining the relationship between Neanderthals and AMH, their phylogenetic status, and the traces this would have left in present-day populations (Dannemann et al., 2016; Deschamps et al., 2016; Fu et al.,

* Corresponding author. Institut Català de Paleoecologia Human i Evolució Social (IPHES), Campus Sescelades, Edifici W3, Tarragona, Spain.
E-mail addresses: carolinacucart@gmail.com (C. Cucart-Mora), slozano@iphes.cat (S. Lozano), jfernandez@iphes.cat (J. Fernández-López de Pablo).

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2014; Kuhlwilm et al., 2016; Prüfer et al., 2014; Reich et al., 2010). Along with these studies, some models have estimated the amount of interbreeding between the Neanderthals and AMH that would have led to the 1–4% of Neanderthal introgression seen in present-day non-African populations (Currat and Excoffier, 2011; Neves and Serva, 2012).

Despite the transition being, in its essence, a process of interaction between genetically and culturally different populations, very few studies have explicitly examined the causative role of population dynamics on the evolution of the Neandertals' population. Traditionally, researchers looking at the demography of either Neanderthals or AMH populations chose two different approaches: they either constructed mathematical models, or inferred demographic dynamics through an analysis of the archaeological record.

Mathematical models show that small differences in mortality rates could have had dramatic consequences. According to Zubrow (1989) stable population model, a 2% increase in mortality among Neanderthals over AMH could have resulted in their extinction within 30 generations. More recently, Sørensen (2011) mathematically simulated fertility and mortality rates to model the evolution of Neanderthal populations under conditions of changing climate and prey availability. His model suggests that a 1% reduction in mortality through childbirth and hunting accidents among AMH would have allowed their population to grow despite adverse climatic conditions, while the Neanderthals population declined. More recently, different mathematical models have addressed the interaction between AMH and Neanderthals considering palaeoanthropological data. Currat and Excoffier (2011), based on the evidence presented by Green et al. (2010), concluded that, to obtain an introgression rate of between 1 and 4% Neanderthal DNA into present-day populations, the interbreeding success rate (the probability of a successful hybridisation) must have been below 2%. In contrast, Neves and Serva (2012) suggest that a low rate of interbreeding between the two species could have been a consequence of their cultural differences (i.e., culture-based restrictions on interspecific reproduction). These mathematical models address the evolution of demographic variables in a scenario of interaction between the two populations; however, their results have not been validated against the empirical record.

The second approach to the study of demographic dynamics is based on the analysis of the archaeological record. Mellars and French (2011) proposed three proxies (stone tool density, mean-weight density and occupation areas) to reconstruct relative population sizes and density in the south-western France from the Late Middle Palaeolithic to the Aurignacian. They suggested that during Early Upper Palaeolithic, the AMH population was an order of magnitude larger than that of the Neanderthals in the preceding period. Other authors including Bocquet-Appel and Degioanni (2013) have proposed an estimated population size of 5000–70000 Neanderthals, based on demographic data from ethnographic sources using a conservation biology formula. Bocquet-Appel et al. (2005) calculated an AMH metapopulation size (per 100 km^2) for four periods of the European Upper Palaeolithic (Aurignacian, Gravetian, Last Glacial Maximum and Late Glacial). For each of the periods, they back-projected reference population estimates obtained from ethnographic data, with inter-period growth rates based on the number of archaeological sites. They then obtained absolute estimates of metapopulation size by multiplying demographic density with perceived territory size generated by modelling the geographical distribution of sites in south-western France. The resulting AMH population size is 795–12,980 AMH contrasting with the suggested estimate of 80–1300 Neanderthals for the precedent period (Bocquet-Appel and Degioanni, 2013).

Despite the significant contribution of the above-mentioned literature to the inference of demographic dynamics, the methods used present limitations when it comes to identifying the relationship between biology and cultural evolution. The study of the bio-cultural interactions of distinct populations is restricted by the biased nature (involving the limited number of remains, differential deposition, conservation, and recovery processes) of the archaeological record.

Regardless of the method and the geographical framework when we study the transition from the Middle to Upper Palaeolithic three main questions arise: (1) For how long did Neanderthals and AMH co-exist? (2) What was the result of this co-existence in biological/genetic terms? (3) To what extent did climatic and geographical variables influence the size and distribution of the population involved? In order to obtain a better understanding of this process, and therefore, be able to answer these questions, we must seek a multi-factor explanation.

In this paper, we address the first and second questions by focusing on the Transition from the Middle to Upper Palaeolithic on the Iberian Peninsula. We use computational experiments to observe the effects of demographic and mobility patterns on the interaction between Neanderthals and AMH in the region. This allows us to systematically explore the significance of historical contingency (Premo, 2006) and produce testable expectations that can be validated against the archaeological record.

2. The Iberian Peninsula

The Iberian Peninsula plays and important role in the study of the transition from the Middle to Upper Palaeolithic (Baena et al., 2005a, 2005b; Maroto et al., 2012; Schmidt et al., 2012; Wood et al., 2014, Wood et al., 2013a; Zilhão and Trinkaus, 2002) as the southern region has often been claimed to be the *refugium* of the last Neanderthals, while the northern area was contemporaneously occupied by AMH.

The differential distribution of final Mousterian and early Aurignacian complexes recorded in the Iberian archaeological record was first explained through the Ebro Frontier Model (Zilhão, 2006, 2009; Zilhão and Trinkaus, 2002; Zilhão, 2009) This model accounts for a real and lasting spatial segregation between the two techno-complexes, and, given the association of these with different hominid species, it also suggests the co-existence of AMH and Neanderthals. According to the model, in the period between 42 ka BP and 35 ka Cal BP (Zilhão, 2009), both Aurignacian and Mousterian techno-complexes were present in the Iberian Peninsula. The transition in the north of the Ebro Valley is a two-step process. First to emerge was the Chatelperronian, an Upper Palaeolithic techno-complex with Middle Palaeolithic roots, and associated with Neanderthals. At approximately 42 ka Cal BP this was replaced by the Proto-Aurignacian industries associated with AMH. In contrast, south of the Ebro Valley, Middle Palaeolithic industries survived until 35 ka Cal BP, at which point they were replaced by Evolved-Aurignacian.

The model proposes that the interruption of the westward advance of AMH must somehow be related to the fact that the Ebro basin represented a bio-geographical border between the Mediterranean and Euro-Siberian domains. For this reason, competition between the two species did not start until the climatic deterioration of the late MIS 3 began to favour the southward expansion of AMH. The advance followed the same process of cultural interaction and biological admixture (Zilhão, 2006) as operated during the advance of AMH into western Eurasia, and led to the assimilation of the last Neanderthal populations (Zilhão, 2013).

Until the early 2000's this was the only model that accounted for the entire Iberian archaeological record. At that time, a revision of