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

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.

© 2017 Elsevier Ltd. All rights reserved.

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.,

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 km²) 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

the archaeological record highlighted certain inconsistences in the model's formulation relating to the archaeological and chronological record (for a revision see:Vaquero (2006)).

Consequently, alternative interpretations of the Iberian archaeological record were proposed. Some researchers state that the extinction of the Neanderthals and the arrival of AMH were independent processes, suggesting that the disappearance of the former was caused by cold and arid conditions at approximately 28 ka BP (Finlayson et al., 2004; Finlayson, 2004; Jiménez-Espejo et al., 2007). This proposal was a response to the model by D'Errico and Sánchez Goñi (2004), who suggested that Neanderthals become extinct because of competition with AMH. Mallol et al. (2012) also reviewed the lithostratigraphic context of the main archaeological sequences and theorizes that the extinction of Neanderthals and the arrival of AMH were independent processes. Other authors (Baena et al., 2005a, 2005b., Carbonell, et al., 2000.), suggested the regional contemporaneity of Neanderthals in both Northern and Southern Iberia (Baena et al., 2005a, 2005b.) or a mixture of all these scenarios at peninsular scale that would include all the above scenarios (Guy Straus, 2005). Zilhão (2009) responded to the criticism with a list of empirical expectations that, if substantiated, would lead either to the revision or abandonment of the model, and discussed whether those findings had or had not been made, concluding that the model had not been refuted.

The re-evaluation of the radiocarbon framework plays a key role in current debates on the timing of the Neanderthal extinction, the expansion of AMH and for how long they interacted with each other (if ever). However, the introduction of new dating procedures, the consequent revision of the chrono-stratigraphic framework, and the attempt to reconcile old and new dates, leaves us with quite a blurry picture. For instance, in Cova Gran (Lleida, Catalunya), a recent revision allowed researchers to discard a scenario of rapid succession between the Late Mousterian and Early Aurignacian at the site (Martínez-Moreno et al., 2010; Mora et al., 2016). They dated the latest Middle Palaeolithic findings with a minimum age around 42 ka Cal BP. Also, Wood et al. (2014) suggested a date of 42 ka for the appearance of Aurignacian in Northern Iberia − a date broadly consistent with the Western European record − from the datation of Labeko Koba (Arrasate, País Vasco), La Viña (Oviedo, Asturias) and l'Arbreda(Girona, Catalunya). Finally, the revisions of the radio-chronological framework of southern Iberia, carried out by Higham et al. (2014) and Wood et al. (2013b) concluded that the co-existence of Neanderthals and AMH would have not lasted as long as previously thought.

As pointed out in the previous section, the understanding of the transition process of during Middle to Upper Palaeolithic requires a multi-factor approach that considers both cultural and biological variables. In this work, we use agent-based modelling to study the interaction between AMH and Neanderthals on the Iberian Peninsula, taking into account a set of specific demographic and behavioural variables (initial population size, birth and death rates, mobility patterns and barriers preventing hybridation) to discuss the range of possible scenarios that may have led to the extinction of the Neanderthals.

3. Methods

In this paper, we adapted a previous agent-based model constructed by Barton and Riel-Salvatore (2012) in Net Logo (Wilensky and Stroup, 1999) to perform a series of computational experiments on the bio-cultural interaction between AMH and Neanderthals during the Middle to Upper Palaeolithic transition on the Iberian Peninsula. The original model is designed to explore the dynamics of biobehavioural interactions between two populations, and their genetic and demographic consequences. The model is implemented to analyse the effect of interspecific differences in initial population sizes, interaction distances, mating restrictions, and fitness. It also tests the spatial distribution of the original two population and the hybrids resulting from the interaction. The model dynamics consists of three steps that are executed at each simulation generation. During simulations three basic dynamics unfold during each of the simulation generations. First, all agents move within a home range of a given radius with no directionality. Then, they reproduce and die with a probability equal to their birth or death rate (respectively), which are both defined in the range [1,1000]. To our knowledge, this is the only example of an agent-based model applied to the study of such a transition in a regional context.

3.1. Model overview

A number of modifications were introduced relating to the analysis scale and computational code, in order to adapt the original model (Barton and Riel Salvatore, 2012) to our study case. First, we used the Iberian Peninsula as the geographic scenario where the interaction took place. Second, demographic and mobility parameters were calibrated using ethnographic data. Third, we introduced a local mechanism to avoid overpopulation, preventing agents from reproducing when their home range was crowded. Fourth, a new range of genotypic groups was created to obtain a more detailed picture of the population's genetic composition at the end of each run. The following description corresponds to the adapted model. For more details of the adaptation please see the code in the Supplementary materials.

3.1.1. Spatial and chronological framework

The simulated world represents the Iberian Peninsula and southern France to latitude of 43° 36′N. We included the South of France in the model as the region from which the Aurignacian and AMH presumably penetrated the Iberian Peninsula. Our simulation scenario has been constructed using a SRTM digital elevation model of the Iberian Peninsula converted to a binary raster with a cell resolution of 10×10 km^2 where land grids are black and sea grids are white. Agents only move within those grids identified as land.

We established an interaction time between agents of 12.500 years representing 500 generations. Such chronological framework is consistent with the oldest Aurignacian context securely dated in Iberia from Labeko Koba's (41.9−40.6 ka Cal BP) and l'Arbreda (41.6−38.2 ka Cal BP) (Wood et al., 2014) and the Gravetian (c. 30 ka Cal BP). Within this time range Cueva Antón (34−36 ka Cal BP) was take as the reference for the latest Middle Palaeolithic context (Zilhão et al., 2016). Each time step in the model represented a generation of 25 years, meaning that the absolute number of generations in our model was 500, translating to the cited 12.500 years.

3.1.2. Agent specification

Our model was populated by agents representing social units of 25 individuals, the average number of individuals in ethnographically-documented hunter-gatherer units (Kelly, 2007). Each agent was characterised by a simple genome of 10 pairs of alleles. There was no directionality in the movement of agents (i.e., they did not migrate towards a particular destination), although they were constrained within a home range of a given radius that could be varied to recreate different mobility strategies.

Initially, the agents were assigned to two genetically distinct groups: Neanderthals (NN) and AMH (MM). All the alleles in the agents from the former group were Neanderthals (i.e. N_iN_i) and were initially confined to the territory south of the Ebro Valley. In contrast, all of the alleles of the agents of the second group were modern (i.e. M_iM_i) and these were initially distributed to the north

of the Ebro Valley. This distribution pattern is based on the Ebro Frontier model as proposed by Zilhão (2009), although it should be noted that the distribution of agents within these two areas does not represent the location of actual archaeological sites.

The starting size of the two groups was calculated taking into account the extent of their initial distribution area together with population density estimates from ethnographic data. Specifically, based on Bocquet-Appel et al. (2005), we applied a density of 0.72 and 0.5 inhabitants per km^2 for AMH and Neanderthals, respectively. Our decision on the lower density of Neanderthals' was based on diverse papers looking at demographic proxies (Bocquet-Appel et al., 2005; Mellars and French, 2011; Bocquet-Appel and Degioanni, 2013), as well as, and archaeo-genetics (Mellars and French, 2013; Fabre et al., 2009; Lalueza-Fox et al., 2012). As a result, the initial scenario was populated by 103 AMH and 114 Neanderthal agents.

When agents mated and produced offspring (see Reproduction routine in section 3.1.4) the new agent was assigned to a genotypic group. These groups (Fig. 1) were denominated 1 to 8, representing the number of modern alleles present in agents' genome. Genotypic groups 1 and 8 correspond to pure Neanderthals and AMH groups, respectively, and genotypic groups 2 to 7 represent hybrids with different ratios of modern alleles.

3.1.3. Assignment of parameters values using ethnographic studies

We used ethnographic data as a reference to obtain the parameter values for our experiments. The uniformitarian nature of demographic processes justifies their use for Anatomically Modern Humans, despite being a fragmentary and biased data source (French, 2016; Kelly, 2007; Howell, 1979). Concerning, Neanderthals and hybrids (i.e. non modern hominins) we adjusted the data according to the parameters suggested by the paleo-anthropological record, following the procedure detailed below.

In our model, the agents' home range is confined into a virtual area of 5 × 5 cells (2500 km^2). Such an estimate is based on ethnographically documented hunter-gatherers inhabiting sub-tropical areas with foraging systems mainly focused on terrestrial resources, particularly medium size ungulates (O'Connell et al., 1988). Because latitude and environment have significant effects on hunter-gatherers' mobility patterns (Binford, 2001; Grove, 2009), we decided to avoid ethnographic examples from artic and sub-artic areas heavily dependent on migratory game such as reinder since such a species of game is minimally represented on most of the Iberian Peninsula during the Late Middle Palaeolithic. In turn, we also decided to exclude home range references of hunter-gatherer's groups heavily dependent on aquatic and littoral resources in Boreal and Subtropical environments which tend to exhibit smaller home range sizes and higher population densities than foragers whose economic systems depend on terrestrial game (Kelly, 2007).

Our starting point for the demographic variables (i.e. birth and death rate), were the Total Fertility Rates-the average number of children that would be born to a woman over her lifetime (Howell, 1979)-compiled by Kelly (2007). The data available on mortality rates is fragmented, and growth rate values are highly variable across historical hunter-gatherer populations. Consequently, given the limitation of data sources, we had to define our value ranges by following a three-step process:

1. As documented Total Fertility Rates range from 2 to 8 offspring, we chose 5, the median, as the reference value for birth rate.
2. We performed preliminary experiments with a fixed birth rate and various values for mortality rate (4, 3, 2 and 1), and recorded final meta-population size (i.e., number of agents).
3. We calculated the corresponding growth rates and checked that these did not exceed the values recorded for historical hunter-gatherer. Such a growth rate was calculated as:

$$PRG = \frac{P(t_2) - P(t_1)}{120\, P(t_1)(t_2 - t_1)}$$

Where PRG corresponds to meta-population growth rate and, P (t) is meta-population size at time t.

From the analysis of the preliminary experimental results, we established 5 and 2 as the reference values for the birth and death rates, respectively.

3.1.4. Model dynamics

According to the original model by Barton and Riel-Salvatore (2012), at each time step in the simulation, all agents perform the following actions:

1) *Move*: every agent moves from its patch to another patch in a random direction for a random distance that is less than or equal to its home range.
2) *Reproduce*: an agent will only reproduce if there is at least one empty patch within its home range. We introduced this condition to avoid overpopulation at a local scale. If there is space, the agent reproduces with a probability equal to its birth-rate.

When an agent reproduces, it looks for a potential mate within its home range. If there is more than one available mate, the selection of one over the other is dependent upon the avoidance option (explained below). Otherwise, if the potential mates are identical, or avoidance has a value of 0, the mate is chosen randomly. When two agents mate, the offspring's genome has an equal chance of receiving alleles on chromosome 1 or 2 from either "parent". If another agent is not found, it clones itselfe. The new agent will establish itself in an empty patch within a distance equal to or greater than its "parental" home range.

Avoidance option applies equally to all agents which show different degrees of assortative mating preferences. With 100% avoidance, the chance that a pair will reproduce depends on the degree of similarity between their genomes. When two different agents reproduce, their genomes combine through independent assortment to create the genome of their offspring.

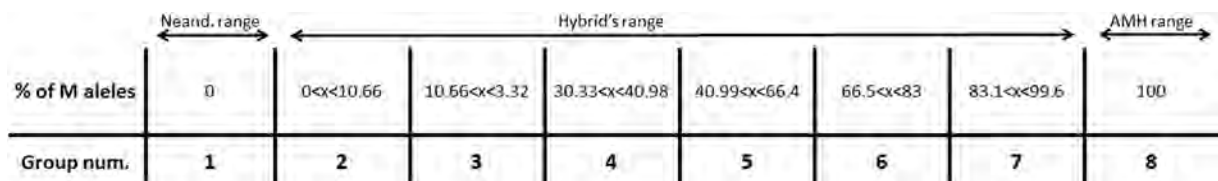3) *Die*: an agent dies with probability equal to its death rate.

% of M aleles	0	0<x<10.66	10.66<x<3.32	30.33<x<40.98	40.99<x<66.4	66.5<x<83	83.1<x<99.6	100
Group num.	1	2	3	4	5	6	7	8

Fig. 1. Genotypic groups and their corresponding range of M alleles, from the variable genome.

3.2. Experimental setting

In our experiments, we simulated the long-term demographic consequences of several bio-behavioural characteristics often mentioned in the literature, relating to the substitution of Neanderthals by AMH. Fig. 2 shows all the scenarios covered by our simulations. For these experiments, we established two experimental rounds: the first was designed to explore the influence of different growth rates on the meta-population's genetic composition; the second was to observe how different mobility strategies (expressed as the size of an agent's home range) modified the results of the previous round.

In relation to interspecific mating we considered evidence derived from palae-genetic studies. Green et al. (2010) estimated that between 1 and 4% of the Eurasian genome is derived from Neanderthals, suggesting a limited amount of interbreeding between the two species. Nevertheless, the authors noted some possible scenarios where interbreeding could have been intense while leaving little trace in present-day populations. We also know that interbreeding between these two species would have not been an exceptional episode of inter-specific mating since more recent studies have shown that AMH and Neanderthals also interbred with Denisovans, and later, with another unknown hominid (Dannemann et al., 2016; Deschamps et al., 2016; Kuhlwilm et al., 2016; Prüfer et al., 2014; Reich et al., 2010). Therefore, accepting the available evidence but considering that paleo-genetic data is still limited, we decided to explore three different scenarios relating to socially mediated restriction of reproduction. As can be observed in Fig. 2 (columns) these correspond to none (0%), low (25%) or high (95%) levels of avoidance. In the first scenario, there are no restrictions to hybridisation; in the second, the restrictions on interspecific reproduction are low with an avoidance levels of 25%; and in the final scenario there are strong barriers against hybridisation with 95% avoidance.

In first round of experiments, the design took into account palaeo-anthropological literature about reconstructing certain aspects of the demographic characteristics of Neanderthal and AMH populations. Several studies suggest differences in mortality patterns of the two populations. The low life expectancy of Neanderthals was suggested by Bocquet-Appel and Degioanni (2013), and Trinkaus (1995). In addition, Caspari and Lee (2004) proposed that AMH had "increased longevity" when compared to Neanderthals. Moreover, the relative abundance of infant remains associated with Middle Palaeolithic contexts has been interpreted as evidence for higher infant mortality rates among Neanderthals (Trinkaus, 1995; Riel-Salvatore and Clark, 2001). On the other hand, studies on faunal remains and stable isotopes (Hockett and Hawkes, 2005; Stiner et al., 2000) suggest that dietary differences would have favoured higher survival rates of AMH offspring and nursing mothers, resulting in higher life expectancy and less infant mortality.

In this round, we also analysed the effect of different growth rates of hybrids on the meta-population's genetic composition. In our model, we defined a hybrid as an individual whose DNA had a certain degree of Neanderthal genetic introgression. This is consistent with the few examples documented in the palaeo-anthropological record (Fu et al., 2014, Fu et al., 2015). Here we decided to test the validity of the model proposed by Currat and Excoffier (2011) which explains the low levels of Neanderthal ancestry in present-day Eurasians as a consequence of low rates of interbreeding, potentially explained by a very strong avoidance of interspecific mating, low fitness of hybrids, or both.

For the second round of experiments, we explored the effects of different mobility strategies, doubling the home range size of all the agents. Here, we followed the assumption presented by Barton and Riel-Salvatore (2012) on the relationship between the logistic or residential mobility patterns of hunter-gatherers with the differential density of retouched tools from MIS 3 lithic assemblages in western Eurasia. According to that study, hominids became increasingly reliant on logistical mobility strategies increasing the size of their home range size. According to ethnographic studies (Kelly, 2007; Binford, 2001), there is a general although not exclusive tendency for logistical mobility systems to cover greater areas than residential mobility strategies. To observe how different mobility strategies could have affected the interaction between Neanderthals and AMH, we explore a set of scenarios where all agents in the model displayed residential mobility (small home range size) and a different set of scenarios where they all displayed logistical mobility (larger home range size). It could be argued that assuming homogeneity in mobility strategies is an over-simplification. For this reason, we designed and executed experiments where only one of each genotypic group displayed a different mobility strategy to the other groups. The results revealed no significant differences between an increased home range size of
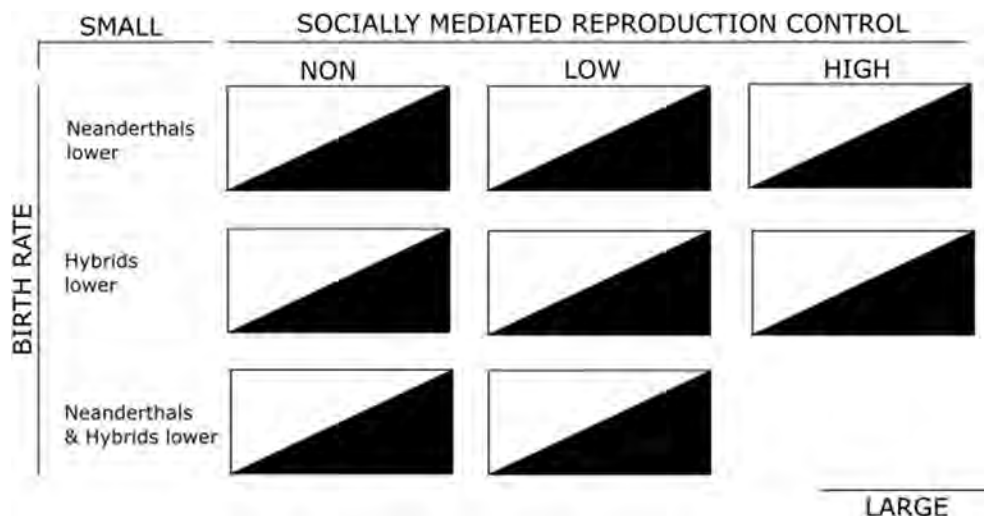

Fig. 2. Different parameters combinations that were used to set the different experiments reported below. Combination of birth rate (rows), different avoidance options (columns), and home range size (upper left and lower right). For the precise parameter values Supplementary materials, Table. S1.

a single genotypic group and a comparable increase in the entire set.

Given the stochastic nature of the model we ran each experiment 50 times, which we found was enough to capture the full variability of the model dynamics.

4. Results

As explained above, we carried out several computational experiments combining different parameter values, to reproduce distinct possible scenarios. The different parameter combinations that were analysed (scenarios) are listed in the Supplementary material, Table.S1. The most relevant results are summarized in this section, nevertheless all results are included in the Supplementary materials, Figure S1 to S6 and table S2. Given the exploratory nature of this work, the main objective when analysing the simulation results was to assess and characterise the effect of the different parameters on: (1) the final meta-population composition (i.e., the number of agents at the end of the simulation in each of the defined genotypic groups); (2), the temporal evolution of pure Neanderthals population size (genotypic group number 1). All statistical analyses were performed using R © 2009—2015 RStudio, Inc. version 0.99.463.

4.1. Final meta-population composition

To compare the variation in the final size of genotypic group across the scenarios, we first constructed boxplots to identify variations associated with different birth rates, avoidance values and home range sizes. Later, to assess the significance of the identified differences we applied Kruskal-Wallis tests.

4.1.1. Effect of growth rate
Here we compare those scenarios where Neanderthals or hybrids genotypic groups alternatively displayed a low growth rate with scenarios where the growth rate was stationary. At first sight, the boxplots (Supplementary material. Table. S1 to S6.) show no obvious differences in meta-population compositions related to changes in group growth rate. Nevertheless, when the Kruskal-Wallis test is applied to the genotypic group size, we can see significant changes. In those scenarios where Neanderthals growth rate is stationary, we can see a significant decrease in the number of agents in groups 1 to 4 and an increase in group 6. As expected, the lower growth rate of Neanderthals group affects not only the number of their own genotypic group, but also, the number of agents in those genotypic groups defined by a high ratio of Neanderthal alleles. This pattern can be observed in experiments 2.B and 2.E. (Fig. 3). On the other hand, when analysing the scenarios where agents display a stationary or low growth rate no significant changes are observed.

4.1.2. Effect of avoidance
The avoidance value has no significant effect on meta-population composition, when hybrid groups have the lowest growth rates, or, in those scenarios where the Neanderthal genotypic group displays a low but positive growth rate (eg., 2.A., 2.B., and 2.C. See Supplementary material, Fig. S2). Nevertheless, a pattern is observed in those scenarios where high avoidance coincides with a zero Neanderthal growth rate, the number of agents in each genotypic group increases as the get close to group number 8 (i.e., AMH).

4.1.3. Effect of home range size
The effect of a large home range on meta-population composition is the same independently on which is the genotypic group

with the lowest growth rate (i.e. either Neanderthals or hybrids). When the genotypic groups in the hybrid range display the lowest growth rate, we can see a significant decrease in the size of groups 1, 2, 7 and 8 in those scenarios with a larger home range. The same effect is observed when Neanderthals genotypic group display the low growth rate. On the other hand, when Neanderthals display a zero-growth rate there is a decrease in the size of groups 2, 3 and 4 associated with an increase in the size of groups 7 and 8 which is confirmed by the Kruskal-Wallis test.

4.2. Temporal evolution of neanderthals group size

We also collected data on the temporal evolution of all genotypic group sizes (i.e., diachronic changes in the number of agents within a genotypic group) throughout the simulations. Nevertheless, for the purpose of this paper we were more interested in the temporal evolution of the Neanderthal genotypic group. In particular, we wanted to know after how many generations Neanderthals disappeared from the simulations, because this can be compared with the radiocarbon record for the disappearance of Neanderthals in the Iberian Peninsula.

In order to analyse the temporal evolution of the size of Neanderthal size, we first constructed line graphs to visualise possible patterns. After this, we calculated the maximum and minimum sizes of the genotypic group and identified the generation number when these extreme values were reached. This last step helped us quantitatively assess the observed patterns and the parameters responsible for them.

In general, the temporal evolution of the Neanderthals group size follows a recognisable pattern in most of our scenarios. The number of agents increases rapidly to reach a maximum group size between generation 40 and 70 (with the median in generation 60), followed by a monotonic decline results in the minimum Neanderthal group size somewhere between 100 and 200 generations of the simulation. This, seems to be a point of no-return, since the Neanderthal group size does not grow again in the 400 remaining generations: it either stabilises or declines until it disappears completely.

4.2.1. Effect of growth rate
As for the effect of growth rate, we can see differences between the scenarios where Neanderthals display a positive growth rate and those where their growth rate is stationary. Positive growth rates are associated with higher maximum group sizes (ca. 1800—2500 agents), which are reached early on the simulation (between generations 40 or 60 simulation generations): the minimum genotypic group size is reached between generations 160 and 190. In contrast, stationary growth rates are associated with a maximum group size of around 900 and 2000 agents, reached at the very beginning of the simulation. Later, in these scenarios the Neanderthal group size decreases until they disappear around 200 generations. This pattern is observed in all simulated scenarios where the Neanderthal genotypic group displays a lower growth rate than the other genotypic groups. On the other hand, the growth rate of hybrids groups has some influence on Neanderthal maximum group size, which increases in those scenarios where hybrids display a stationary growth rate. As an example, in experiment 1.A. Neanderthal's average maximum group is 196, where in experiment 1.D. It is 204 (see Supplementary materials, Table S2). In contrast, there is no influence on minimum group size or generation number when these extreme values are reached.

4.2.2. Effect of avoidance
There is a positive relationship between the avoidance value and the maximum group size reached by Neanderthals in the
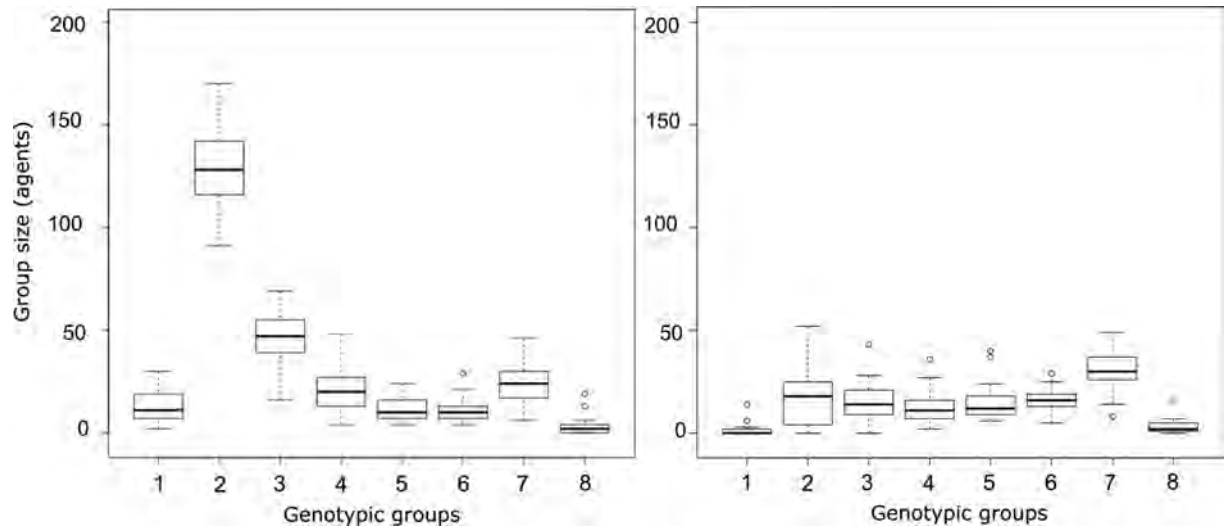
Fig. 3. Median and midspread of genotypic group sizes at the end of the simulation after 50 iterations. For details on the parameter values of experiments 2.B (right) and 2.E (left), see Supplementary materials, Table. S1.
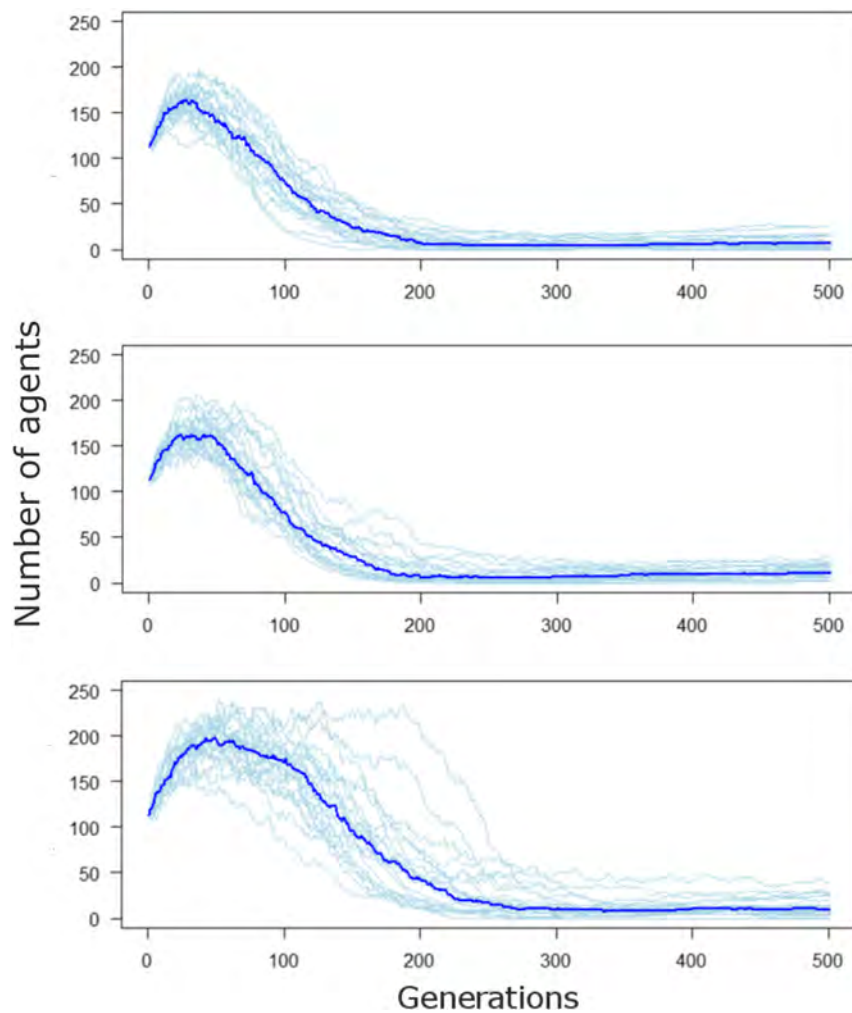
Fig. 4. Temporal evolution of Neanderthal group size after 50 iterations. Light blue represents the temporal evolution of each of the 50 iterations, dark blue is, the median value for the temporal evolution of Neanderthal group size. For details on experimental parameters for 2.A. (top) avoidance 25%, 2.B. (middle) avoidance 75%, and 2.C (bottom) avoidance 95%. See Table S1. Supplementary materials. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

simulation. This relationship can be observed in Fig. 4. Noteworthy the same pattern is observed in relation to minimum group size, which is higher and reached in later generations as avoidance value increases. This pattern is similar in all scenarios, no matter the genotypic group having the lowest growth rate.

Fig. 4 also shows the effect of avoidance over the variability of results. In particular, we observe a wider variability of the temporal evolution of Neanderthals group size as the avoidance value increases (from top to bottom). This phenomenon can be explained from the combined effect of high avoidance value and the spatial distribution of agents. As the avoidance value increases, the chance for reproduction with agents from other genotypic groups are reduced (or, in other words, more agents increase the probability of Neanderthals agents of reproducing). Consequently, in those simulations iterations where Neanderthals agents do not have enough non-Neanderthals neighbours, they clone themselves. When this happens, Neanderthal population can delay the dilution of its genotype. This is especially visible in Fig. 4 bottom, where the Neanderthal population stabilizes its size between generation 50 and 230 (depending on the simulation iteration). In other iterations, Neanderthals agents find themselves surrounded by agents similar enough to reproduce with. In these cases, Neanderthal pure genotype dilutes as they reproduce with other agents, consequently, we observe a decline in the number of Neanderthals agents that begins between generations 50 and 100.

4.2.3. Home range size

Home range size has a significant effect on Neanderthal groups size. First, we observe a reduction in the maximum size reached by genotypic group 1. In no scenario does the Neanderthals group reach a maximum of more than 135 agents, when in analogous cases defined by a small home range, the maximum group size reaches values between 170 and 200 agents (see Supplementary materials, Table. S2). This means, the inter-specific interaction of agents results in a quick "dilution" of the Neanderthal genotype. Remarkably, when a large home range is combined with a zero growth rate we do not see the characteristic initial increase in group size. Instead, the Neanderthal group size decreases right from the beginning of the simulation and Neanderthals disappear between generations around generation 120 and 150 (eg., 5.D. Fig. 5). A fairly similar pattern is observed when the hybrid genotypic groups have the lowest growth rate.

5. Discussion and conclusions

The demise of the Neanderthals was not a simple, lineal process (Villa and Roebroeks, 2014). Their disappearance from the

archaeological record can only be explained through the interaction of several factors. This complexity requires a multi-approach analysis; the study of the transition from the Middle to Upper Palaeolithic has been addressed by a wide range of disciplines, including archaeology, physical anthropology, genetics, chronometry, and palaeo-environmental analyses. To satisfactorily understand this process, several approaches (and their corresponding evidence and data sources) must be considered.

In this paper, we have presented a bottom-up approach to computational modelling in which the model is constructed from its component features in order to observe the results of their interactions. Such an approach can help us better understand the relationships between different data sources and uncover patterns of interaction between various factors. We applied this approach to study the possible effect of demographic behaviour and mobility patterns on the demise of the Neanderthals.

Specifically, we adapted a previously published model (Barton et al., 2011) to a regional scale. In doing so, we used ethnographic data to calibrate birth and death rates, define the extent of the agents' home ranges and establish the initial number of Neanderthal and AMH agents. Next, we used the resulting models to perform computational experiments testing multiple combinations of parameter values. Two types of results were recorded: the size of the different genotypic groups at the end of simulation: and the temporal evolution of Neanderthals' genotypic group size.

Our results suggest that disappearance of the Neanderthals could be explained by inter-specific differences in demographic behaviour and mobility patterns compared to AMH. Concretely, this scenario is defined by Neanderthal groups having a lower growth rate than AMH and hybrids; agents moving within large home ranges: and moderate or high culturally-mediated barriers preventing inter-specific reproduction.

From a broad perspective, our model results are aligned with those models that suggest that the success of AMH over Neanderthals was a result of the fitness advantage of the former (Klein, 2008; Mellars, 2005; Stiner and Munro, 2002; Kuhn and Stiner, 2006). More concretely, our results suggest that the demise of Neanderthals could be related to an even small fitness advantage of AMH. Moreover, the effect of hybridation and a large home range are highly relevant to explain our results and their match with the chronological framework for the demise of Neanderthals in Iberia.

At a peninsular scale, our results are consistent with the current radiocarbon framework for the disappearance of Neanderthals in Iberia. Since the late 80's the centre and south of the Iberian Peninsula has been considered a refugee for the last Neanderthals who survived long after the arrival of the AMH north of Iberia. More recently, some authors have suggested that Neanderthals survived
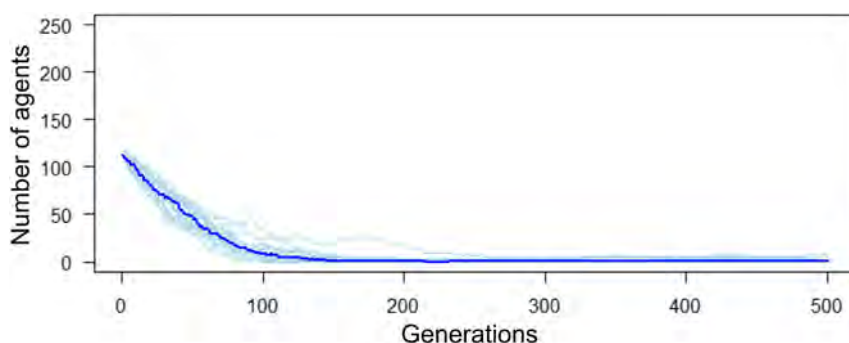

Fig. 5. Temporal evolution of Neanderthal group size after 50 iterations. Light blue represents the temporal evolution of each of the 50 iterations, dark blue is, the median value for the temporal evolution of Neanderthal group size. For details on experimental parameter values 5.D. see Table. S1, and S2 in the Supplementary materials. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

South of the Ebro Valley until 36.7—34.5 Ka cal BP (Cueva Anton), while others extend this date until 32—28 ka cal BP (Gorham's Cave). On the other hand, a major re-evaluation of the stratigraphically contexts and the application of new dating procedures has questioned the fact that Neanderthals in Iberia survived much longer than anywhere else in Europe (Wood et al., 2013a; Higham, et al., 2014; Alcaraz-Castaño et al., 2017). Among others Wood et al. (2013a) and Maroto et al. (2012) suggest that Neanderthals and AMH did not co-exist in the Iberian Peninsula. Nevertheless, some sites in the Atlantic and Mediterranean Southern coasts, still suggest a post 42 ka cal BP survival for Neanderthals. Dates obtained at Oliveira, Cueva Anton and Sima de las Palomas remain unchallenged concerning the integrity of the chronometric results.

Our model results support both a rapid expansion of the modern genotype and a late survival of some Neanderthals group survive isolated at the Southern extremes of the Iberian Peninsula. These isolated groups eventually disappeared within a chronological framework that coincides with the dates provided by Cueva Antón. The demise of Neanderthals in our model is based on (slight) differences in demographic growth, and the relocation of AMH and hybrid groups in adjacent patches leaving Neanderthal agents isolated and unable to reproduce. The relevance that migration and relocation of AMH groups or bands could have had in the extinction of Neanderthals, has also recently been, pointed out by Kolodny and Feldman (2017). Our approach to the mobility of hunter-gatherer groups provides an alternative explanation for the particular chronological framework of the transition in the Iberian Peninsula.

The Ebro Frontier (Zilhão and Trinkaus, 2002) suggests that this chronological framework resulted from the environmental differences between the North and South of the Ebro Valley. At a first stage, these differences would have refrained the Southward advance of AMH, allowing the survival of Neanderthals south of the Valley. At a second stage, once the environmental conditions changed, and AMH would have resumed their advance assimilating Neanderthals. In this work, experiments have quantitatively shown that this chronological framework can be matched considering non-oriented, and continued, migration and relocation of human groups.

The results obtained in our computational experiments provide expectations to be tested through archaeological research. In particular, we observed an early disappearance of the Neanderthal genotype (between 100 and 200 generation). Therefore, we could expect to find a decline in the frequency of late Middle Palaeolithic sites and paleo-anthropological remains during this final stage. In addition, according to our modelling results it could be expected an earlier disappearance of the late Middle Palaeolithic contexts in those areas closer to the contact border (i.e. Ebro Valley) than in the more distant areas (i.e. southernmost extreme of the Iberian Peninsula). The ongoing re-evaluation of the Iberian chronostratigraphic contexts will validate (or not) these expectations. A confirmation of these expectations would reinforce the explanatory power of our simulated interaction scenario. Otherwise, if they were not met, we should re-define our model and experimental settings under the light of new theoretical framework and evidences.

On the other hand, our results partially match with current archaeological evidences that suggests a very limited degree of Neanderthal genetic introgression into the AMH genome. In the experiments resulting in the disappearance of Neanderthals, meta-population is composed of a remarkable number of hybrid agents. Nevertheless, these agents show a limited level of Neanderthal introgression in their genomes. This leads us to think that there are other parameters that could have had an effect on the result of the interaction between Neanderthals and AMH.

Different studies (Mellars, 2005; Schmidt et al., 2012; Jiménez-Espejo et al., 2007; D'Errico, 2003; Finlayson and Carrión, 2007) suggest that the changing climatic conditions at the end of MIS 3 could have had a major influence on the disappearance of the Neanderthals. Further developments of this model will integrate geographical and ecological variability, in order to better understand how these parameters could have influenced meta-population dynamics.

Our interest lies in improving our knowledge of and insight into the bio-cultural interactions between Neanderthals and AMH, an area where agent-based modelling has proven to a valuable tool. To make our work replicable and allow other scientist to further apply and develop the model we have included the associated data files in the Supplementary materials and have uploaded the Net Logo code to Open ABM (https://www.openabm.org/model/5271/version/1/view).

Formatting and funding sources

Acknowledgments

Appendix A. Supplementary data

Supplementary data related to this article can be found at https://doi.org/10.1016/j.jas.2017.11.001.

References

Alcaraz-Castaño, M., Alcolea-González, J., Kehl, M., Albert, R.-M., Baena-Preysler, J., de Balbín-Behrmann, R., Cuartero, F., Cuenca-Bescós, G., Jiménez-Barredo, F., López-Sáez, J.-A., Piqué, R., Rodríguez-Antón, D., Yravedra, J., Weniger, G.-C., 2017. A context for the last Neandertals of interior Iberia: los Casares cave revisited. PLoS One 12, e0180823.

Baena, J., Carrión, E., Ruiz, B., Ellwood, B., Sesé, C., Yravedra, J., Jordá, L., Uzquiano, P., Velazquez, R., Manzano, I., Sánchez-Marco, A., Hernández, F., 2005a. Paleo-ecologia y comportamiento humano durante el Pleistoceno superior en la comarca de Liébana: la sequencia de la cueva del Esquilleu (Cantabria, España). In: Lasheras, J.A., Montes, R. (Eds.), Neandertales cantábricos. Estado de la cuestión., Museo de Altamira. Ministerio de Cultura, Madrid, pp. 461—487.

Baena, J., Carrión, E., Velázquez, R., Manzano, I.G., 2005b. Ocupaciones musterienses en la comarca de Liébana (Occidente de Cantabria, España). ADEMA, Soria.

Barton, C.M., Riel-Salvatore, J., 2012. Agents of change: modeling biocultural evolution in upper pleistocen in western Eurasia. Adv. Complex Syst. 15, 1150003.

Barton, C.M., Riel-Salvatore, J., Anderies, J.M., Popescu, G., 2011. Modeling human ecodynamics and biocultural interactions in the late pleistocene of western Eurasia. Hum. Ecol. 39, 705—725.

Binford, L., 2001. Constructing Frames of Reference. An Analytical Method for Archaeological Theory Building Using Ethnographic and Environmental Data Set. University of California Press, California.

Blasco, R., Rosell, J., Rufa, A., Sánchez Marco, A., Finlayson, C., 2015. Pigeons and choughs, a usual resource for the Neanderthals in Gibraltar. Quat. Int. 421, 62—77.

Bocquet-Appel, J.-P., Degioanni, A., 2013. Neanderthal demographic estimates. Curr. Anthropol. 54, S202—S213.

Bocquet-Appel, J.-P., Demars, P.-Y., Noiret, L., Dobrowsky, D., 2005. Estimates of Upper Palaeolithic meta-population size in Europe from archaeological data. J. Archaeol. Sci. 32, 1656—1668.

Carbonell, E., Vaquero, M., Maroto, J., Rando, J.M., Mallol, C., 2000. A Geographic perspective on the Middle to upper Paleolithic transition in the Iberian peninsula. In: Bar-Yosef, O., Pilbeam, D.I. (Eds.), The Geography of Neandertals and Modern Humans in Europe and the Greater Mediterranean. Harvard University, Cambridge.

Caspari, R., Lee, S.-H., 2004. Older age becomes common late in human evolution. Proc. Natl. Acad. Sci. U. S. A. 101, 10895—10900.

Collard, M., Vaesen, K., Cosgrove, R., Roebroeks, W., 2016. The empirical case against the 'demographic turn' in Palaeolithic archaeology. Philosophical Trans. R. Soc. B Biol. Sci. 371.

Conard, N.J., 2003. Palaeolithic ivory sculptures from southwestern Germany and the origins of figurative art. Nature 426, 830—832.

Currat, M., Excoffier, L., 2011. Strong reproductive isolation between humans and Neanderthals inferred from observed patterns of introgression. Proc. Natl. Acad. Sci. 108, 15129—15134.

D'Errico, F., 2003. The invisible frontier. A multiple species model for the origin of behavioral modernity. Evol. Anthropol. Issues, News, Rev. 12, 188—202.

D'Errico, F., Stringer, C.B., 2011. Evolution, revolution or saltation scenario for the emergence of modern cultures? Philosophical Trans. R. Soc. Lond. B Biol. Sci. 366, 1060—1069.

Dannemann, M., Andrés, Aida M., Kelso, J., 2016. Introgression of neandertal- and denisovan-like haplotypes contributes to adaptive variation in human toll-like receptors. Am. J. Hum. Genet. 98, 22—33.

Deschamps, M., Laval, G., Fagny, M., Itan, Y., Abel, L., Casanova, J.-L., Patin, E., Quintana-Murci, L., 2016. Genomic signatures of selective pressures and introgression from archaic hominins at human innate immunity genes. Am. J. Hum. Genet. 98, 5—21.

D'Errico, F., Sánchez Goñi, M.a.F., 2004. A Garden of Eden for the Gibraltar Neandertals? A reply to Finlayson et al. Quat. Sci. Rev. 23, 1210—1216.

Fabre, V., Condemi, S., Degioanni, A., 2009. Genetic evidence of geographical groups among Neanderthals. PLoS One 4, e5151.

Finlayson, C., 2004. Neanderthals and Modern Humans. An Ecological and Evolutionary Perspective. Cambridge University Press, Cambridge.

Finlayson, C., Carrión, J.S., 2007. Rapid ecological turnover and its impact on Neanderthal and other human populations. Trends Ecol. Evol. 22, 213—222.

Finlayson, C., Fa, D.A., Finlayson, G., Pacheco, F.G., Vidal, J.Rg., 2004. Did the moderns kill off the Neanderthals? A reply to F. d'Errico and Sánchez Goñi. Quat. Sci. Rev. 23, 1205—1209.

Finlayson, C., Brown, K., Blasco, R., Rosell, J., Negro, J.J., Bortolotti, G.R., Finlayson, G., Sánchez Marco, A., Giles Pacheco, F., Rodríguez Vidal, J., Carrión, J.S., Fa, D.A., Rodríguez Llanes, J.M., 2012. Birds of a feather: neanderthal exploitation of raptors and corvids. PLoS One 7, e45927.

Fiore, I., Gala, M., Romandini, M., Cocca, E., Tagliacozzo, A., Peresani, M., 2014. From feathers to food: reconstructing the complete exploitation of avifaunal resources by Neanderthals at Fumane cave, unit A9. Quat. Int. 421, 134—153. https://doi.org/10.1016/j.quaint.2015.11.142.

French, J.C., 2016. Demography and the palaeolithic archaeological record. J. Archaeol. Method Theory 23, 150—199.

Fu, Q., Li, H., Moorjani, P., Jay, F., Slepchenko, S.M., Bondarev, A.A., Johnson, P.L.F., Aximu-Petri, A., Prüfer, K., de Filippo, C., Meyer, M., Zwyns, N., Salazar-Garcia, D.C., Kuzmin, Y.V., Keates, S.G., Kosintsev, P.A., Razhev, D.I., Richards, M.P., Peristov, N.V., Lachmann, M., Douka, K., Higham, T.F.G., Slatkin, M., Hublin, J.-J., Reich, D., Kelso, J., Viola, T.B., Paabo, S., 2014. Genome sequence of a 45,000-year-old modern human from western Siberia. Nature 514, 445—449.

Fu, Q., Hajdinjak, M., Moldovan, O.T., Constantin, S., Mallick, S., Skoglund, P., Patterson, N., Rohland, N., Lazaridis, I., Nickel, B., Viola, B., Prüfer, K., Meyer, M., Kelso, J., Reich, D., Paabo, S., 2015. An early modern human from Romania with a recent Neanderthal ancestor. Nature 524, 216—219.

Green, R.E., Krause, J., Briggs, A.W., Maricic, T., Stenzel, U., Kircher, M., Patterson, N., Li, H., Zhai, W., Fritz, M.H.-Y., Hansen, N.F., Durand, E.Y., Malaspinas, A.-S., Jensen, J.D., Marques-Bonet, T., Alkan, C., Prüfer, K., Meyer, M., Burbano, H.A., Good, J.M., Schultz, R., Aximu-Petri, A., Butthof, A., Höber, B., Höffner, B., Siegemund, M., Weihmann, A., Nusbaum, C., Lander, E.S., Russ, C., Novod, N., Affourtit, J., Egholm, M., Verna, C., Rudan, P., Brajkovic, D., Kucan, Ž., Gušic, I., Doronichev, V.B., Golovanova, L.V., Lalueza-Fox, C., de la Rasilla, M., Fortea, J., Rosas, A., Schmitz, R.W., Johnson, P.L.F., Eichler, E.E., Falush, D., Birney, E., Mullikin, J.C., Slatkin, M., Nielsen, R., Kelso, J., Lachmann, M., Reich, D., Pääbo, S., 2010. A draft sequence of the neandertal genome. Science 328, 710—722.

Grove, M., 2009. Hunter—gatherer movement patterns: causes and constraints. J. Anthropol. Archaeol. 28, 222—233.

Guy Straus, L., 2005. A mosaic of change: the Middle—Upper Paleolithic transition as viewed from New Mexico and Iberia. Quat. Int. 137, 47—67.

Hardy, B.L., Moncel, M.-H., Daujeard, C., Fernandes, P., Béarez, P., Desclaux, E., Chacon Navarro, M.G., Puaud, S., Gallotti, R., 2013. Impossible Neanderthals? Making string, throwing projectiles and catching small game during Marine Isotope Stage 4 (Abri du Maras, France). Quat. Sci. Rev. 82, 23—40.

Higham, T., Douka, K., Wood, R., Ramsey, C.B., Brock, F., Basell, L., Camps, M., Arrizabalaga, A., Baena, J., Barroso-Ruiz, C., Bergman, C., Boitard, C., Boscato, P., Caparros, M., Conard, N.J., Draily, C., Froment, A., Galvan, B., Gambassini, P., Garcia-Moreno, A., Grimaldi, S., Haesaerts, P., Holt, B., Iriarte-Chiapusso, M.-J., Jelinek, A., Jorda Pardo, J.F., Maillo-Fernandez, J.-M., Marom, A., Maroto, J., Menendez, M., Metz, L., Morin, E., Moroni, A., Negrino, F., Panagopoulou, E., Peresani, M., Pirson, S., de la Rasilla, M., Riel-Salvatore, J., Ronchitelli, A., Santamaria, D., Semal, P., Slimak, L., Soler, J., Soler, N., Villaluenga, A., Pinhasi, R., Jacobi, R., 2014. The timing and spatiotemporal patterning of Neanderthal disappearance. Nature 512, 306—309.

Hockett, B., Hawkes, J.A., 2005. Nutritional ecology and the human demography of Neanderthal extinction. Quat. Int. 137, 21—34.

Howell, N., 1979. Demography of the Dobe !Kung. Evolutionary Foundations of Human Behavior. Academic Press, New York.

Jiménez-Espejo, F.J., Martínez-Ruiz, F., Finlayson, C., Paytan, A., Sakamoto, T., Ortega-Huertas, M., Finlayson, G., Iijima, K., Gallego-Torres, D., Fa, D., 2007. Climate forcing and Neanderthal extinction in Southern Iberia: insights from a multi-proxy marine record. Quat. Sci. Rev. 26, 836—852.

Kelly, R.L., 2007. The Foraging Spectrum: Diversity in Hunter-Gatherers Lifeways. Cambridge University Press, Cambridge.

Klein, R.G., 2008. Out of Africa and the evolution of human behavior, evolutionary anthropology: issues. News, Rev. 17, 267—281.

Kolodny, O., Feldman, M.W., 2017. A parsimonious neutral model suggests Neanderthal replacement was determined by migration and random species drift. Nat. Commun. 8, 1040.

Kuhlwilm, M., Gronau, I., Hubisz, M.J., de Filippo, C., Prado-Martinez, J., Kircher, M., Fu, Q., Burbano, H.A., Lalueza-Fox, C., de la Rasilla, M., Rosas, A., Rudan, P., Brajkovic, D., Kucan, Ž., Gušic, I., Marques-Bonet, T., Andrés, A.M., Viola, B., Pääbo, S., Meyer, M., Siepel, A., Castellano, S., 2016. Ancient gene flow from early modern humans into Eastern Neanderthals. Nature 530, 429—433.

Kuhn, L., Stiner, C., 2006. What's a mother to Do? The division of labor among Neandertals and modern humans in Eurasia. Curr. Anthropol. 47, 953—981.

Lalueza-Fox, C., Gigli, E., Sánchez-Quinto, F., de la Rasilla, M., Fortea, J., Rosas, A., 2012. Issues from Neandertal genomics: diversity, adaptation and hybridisation revised from the El Sidrón case study. Quat. Int. 247, 10—14.

Mallol, C., Hernández, C.M., Machado, J., 2012. The significance of stratigraphic discontinuities in Iberian Middle-to-Upper Palaeolithic transitional sites. Quat. Int. 275, 4—13.

Maroto, J., Vaquero, M., Arrizabalaga, Á., Baena, J., Baquedano, E., Jordá, J., Julià, R., Montes, R., Van Der Plicht, J., Rasines, P., Wood, R., 2012. Current issues in late middle palaeolithic chronology: new assessments from northern Iberia. Quat. Int. 247, 15—25.

Martínez-Moreno, J., Mora, R., Ignacio de la, T., 2010. The middle-to-upper palaeolithic transition in Cova gran (Catalunya, Spain) and the extinction of Neanderthals in the iberian peninsula. J. Hum. Evol. 58, 211—226.

McBrearty, S., Brooks, A.S., 2000. The revolution that wasn't: a new interpretation of the origin of modern human behavior. J. Hum. Evol. 39, 453—563.

Mellars, P., 2005. The impossible coincidence. A single-species model for the origins of modern human behavior in Europe. Evol. Anthropol. Issues, News, Rev. 14, 12—27.

Mellars, P., French, J.C., 2011. Tenfold population increase in western Europe at the neandertal—to—modern human transition. Science 333, 623—627.

Mellars, P., French, J.C., 2013. Population changes across the Neanderthal-to-modern-human transition in western France: a reply to Dogandžić and McPherron (2013). J. Hum. Evol. 65, 330—333.

Mora, R., Martínez-Moreno, J., Roy Sunyer, M., Benito Calvo, A., Polo-Díaz, A., Samper Carro, S., 2016. Contextual, technological and chronometric data from Cova Gran: their contribution to discussion of the Middle-to-Upper Paleolithic transition in northeastern Iberia. Quat. Int. https://doi.org/10.1016/j.quaint.2016.05.017.

Nash, D., Coulson, S., Staurset, S., Ullyott, J.S., Babutsi, M., et al., 2013. Provenancing of silcrete raw materials indicates long-distance transport toTsodilo Hills, Botswana, during the Middle Stone Age. J Hum Evol 64, 280—288.

Neves, A.G.M., Serva, M., 2012. Extremely rare interbreeding events can explain neanderthal DNA in living humans. PLoS One 7, e47076.

O' Conell, J., Hawkes, K., Blurton Jones, N., 1988. Hadza scavenging: implications for plio-pleistocene hominid subsistence. Current Anthropology 29.

Premo, L.S., 2006. Agent-based Models as Behavioral Laboratories for Evolutionary Anthropological Research.

Premo, L.S., Kuhn, S.L., 2010. Modeling effects of local extinctions on culture change and diversity in the paleolithic. PLoS One 5, e15582.

Prüfer, K., Racimo, F., Patterson, N., Jay, F., Sankararaman, S., Sawyer, S., Heinze, A., Renaud, G., Sudmant, P.H., de Filippo, C., Li, H., Mallick, S., Dannemann, M., Fu, Q., Kircher, M., Kuhlwilm, M., Lachmann, M., Meyer, M., Ongyerth, M., Siebauer, M., Theunert, C., Tandon, A., Moorjani, P., Pickrell, J., Mullikin, J.C., Vohr, S.H., Green, R.E., Hellmann, I., Johnson, P.L.F., Blanche, H., Cann, H., Kitzman, J.O., Shendure, J., Eichler, E.E., Lein, E.S., Bakken, T.E., Golovanova, L.V., Doronichev, V.B., Shunkov, M.V., Dereviank, A.P., Viola, B., Slatkin, M., Reich, D., Kelso, J., Paabo, S., 2014. The complete genome sequence of a Neanderthal from the Altai Mountains. Nature 505, 43—49.

Reich, D., Green, R.E., Kircher, M., Krause, J., Patterson, N., Durand, E.Y., Viola, B., Briggs, A.W., Stenzel, U., Johnson, P.L.F., Maricic, T., Good, J.M., Marques-Bonet, T., Alkan, C., Fu, Q., Mallick, S., Li, H., Meyer, M., Eichler, E.E., Stoneking, M., Richards, M., Talamo, S., Shunkov, M.V., Derevianko, A.P., Hublin, J.-J., Kelso, J., Slatkin, M., Paabo, S., 2010. Genetic history of an archaic hominin group from Denisova Cave in Siberia. Nature 468, 1053—1060.

Riel-Salvatore, J., Clark, G.A., 2001. Grave markers: middle and early upper paleolithic burials and the use of chronotypology in contemporary paleolithic research. Curr. Anthropol. 42, 449—479.

Schmidt, I., Bradtmöller, M., Kehl, M., Pastoors, A., Tafelmaier, Y., Weninger, B., Weniger, G.-C., 2012. Rapid climate change and variability of settlement patterns in Iberia during the Late Pleistocene. Quat. Int. 274, 179—204.

Sørensen, B., 2011. Demography and the extinction of european Neanderthals. J. Anthropol. Archaeol. 30, 17—29.

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

Stiner, M.C., Munro, N.D., Surovell, T.A., 2000. The tortoise and the hare: small game use, the broad spectrum revolution and Paleolithic demography. Curr. Anthropol. 42, 39—73.

Trinkaus, E., 1995. Neanderthal mortality patterns. J. Archaeol. Sci. 22, 121—142.

Vaquero, M., 2006. El tránsito Paleolítico Medio/Superior en la Península Ibérica y la Frontera del Ebro. Comentario a Zilhão. Pyrenae 37, 107—129.

Villa, P., Roebroeks, W., 2014. Neandertal demise: an archaeological analysis of the modern human superiority complex. PLoS One 9, e96424.

Wilensky, U., Stroup, W., 1999. Center for Connected Learning and Computer-Based Modeling. Northwestern University, Evanston, IL. HubNet. http://ccl.northwestern.edu/netlogo/hubnet.html.

Wood, R.E., Barroso-Ruíz, C., Caparrós, M., Jordá Pardo, J.F., Galván Santos, B., Higham, T.F.G., 2013a. Radiocarbon dating casts doubt on the late chronology of the Middle to Upper Palaeolithic transition in southern Iberia. Proc. Natl. Acad. Sci. 110, 2781—2786.

Wood, R.E., Higham, T.F.G., De Torres, T., Tisnérat-Laborde, N., Valladas, H., Ortiz, J.E., Lalueza-Fox, C., Sánchez-Moral, S., Cañaveras, J.C., Rosas, A., SantamarÍA, D., De La Rasilla, M., 2013b. A new date for the Neanderthals from El Sidrón cave (Asturias, northern Spain). Archaeometry 55, 148—158.

Wood, R.E., Arrizabalaga, A., Camps, M., Fallon, S., Iriarte-Chiapusso, M.J., Jones, R., Maroto, J., de la Rasilla, M., Santamaría, D., Soler, J., Soler, N., Villaluenga, A., Higham, T.F.G., 2014. The chronology of the earliest upper palaeolithic in northern Iberia: new insights from L'Arbreda, Labeko Koba and La Viña. J. Hum. Evol. 69, 91—109.

Zilhão, J., 2006. Chronostratigraphy of the middle-to-upper paleolithic transition in the iberian peninsula. Pyrenae 37, 7—84.

Zilhão, J., 2007. The emergence of ornaments and art: an archaeological perspective on the origins of "behavioral modernity". J. Archaeol. Res. 15, 1—54.

Zilhão, J., 2009. The Ebro frontier revised. In: Camps, M., Szmidt, C. (Eds.), The Mediterranian from 50000 to 25000 BP.Turning Points and New Directions. Oxbow books, Oxford.

Zilhão, J., 2013. Neandertal-modern human contact in western Eurasia: issues of dating, taxonomy, and cultural associations. In: Akazawa, T., Nishiaki, Y., Aoki, K. (Eds.), Dynamics of Learning in Neanderthals and Modern Humans, Cultural Perspectives, vol. 1. Springer, Japan, Tokyo, pp. 21—57.

Zilhão, J., Trinkaus, E., 2002. Portrait of the Artist as a Young Child: the Gravetian Human Skeleton from the Abrigo Do Lagar Velho and its Archaeological Context, Lisboa.

Zilhão, J., Ajas, A., Badal, E., Burow, C., Kehl, M., López-Sáez, J.A., Pimenta, C., Preece, R.C., Sanchis, A., Sanz, M., Weniger, G.-C., White, D., Wood, R., Angelucci, D.E., Villaverde, V., Zapata, J., 2016. Cueva Antón: a multi-proxy MIS 3 to MIS 5a paleoenvironmental record for SE Iberia. Quat. Sci. Rev. 146, 251—273.

Zubrow, E., 1989. The demographic modeling of Neanderthal extintion. In: Mellars, P., Stringer, C. (Eds.), The Human Revolution: Behavioral and Biological Perspectives on the Origin of Modern Humans. Edinburg University Press, Edinburg.