World Scientific
www.worldscientific.com

AGENTS OF CHANGE: MODELING BIOCULTURAL EVOLUTION IN UPPER PLEISTOCENE WESTERN EURASIA

C. MICHAEL BARTON* and JULIEN RIEL-SALVATORE[†]

*Center for Social Dynamics and Complexity,
and School of Human Evolution and Social Change,
Arizona State University, USA

[†]Department of Anthropology,
University of Colorado Denver, USA

The complex interactions between social learning and biological change are key to understanding the human species and its origins. Yet paleoanthropological models often focus only on the evolution of the human genome and physical characters, while behavior is treated as an epiphenomenon of biological evolution. We present the results of a series of experiments that use computational models, parametrized with new archaeological data, to simulate the complex dynamics of human biocultural evolution in the changing environment of OIS (Oxygen Isotope Stage) 3 of western Eurasia (∼58000–27000 ka). These experiments allow us to compare alternative trajectories of human evolution, resulting from differing combinations of socioecological behaviors and biological conditions, against the paleoanthropological record.

Keywords: Modeling; Neanderthals; modern human origins; human ecology; Pleistocene hominins; land-use; gene-culture coevolution.

1. Introduction

Humans have a biological history like all other living organisms. But unlike other organisms, it is the combined history of biological and cultural evolution that is essential for understanding the origins of modern humans and their roles in terrestrial ecosystems. For this reason, the study of ancient human behavioral residues — including tools, food remains, and constructed features — has received scientific attention along with the study of human fossils. Modern humans evolved in the context of the late Middle Pleistocene but only began radiating from Africa during the Upper Pleistocene, spanning Oxygen Isotope Stages (OIS) 5-2 (128000–11500 years ago), and recent discoveries and innovative analytical methods continue to provide more detailed information about the biology or behavior of the ancestors of our species [36, 46, 54, 83]. However, the interactions between biology and behavior

have received considerably less attention than the study of genes, fossils, or artifacts, even though the coevolution of underlying genetic and cultural inheritance systems is probably key to many of the most notable characteristics of modern *Homo sapiens*. (See [17, 74, 87, 88, 90] for notable exceptions that do focus on biocultural interactions in human evolution.) For example, beyond the obvious fact that a biological basis is needed for any kind of expressed behavior, biological controls on human language (i.e. not simply the mechanics of speech) have long been recognized, and recent studies also suggest a biological basis for human learning patterns and prosocial behaviors essential for human society and culture [17, 21, 108]. On the other hand, sociality and social learning have long been important environments of selection for biological characteristics; more generally, human behaviors have had — and continue to have — an important impact on human biology and its evolution [27, 74, 75, 84, 90].

Unlike human fossils or artifacts, however, biocultural evolutionary interactions are not preserved in the prehistoric record. They must be modeled as dynamic processes. Nonetheless, such processes may leave indirect signatures in the regional-scale distributions of fossils or behavioral residues, or genetic patterns at population scales [55, 74, 88]. There is consensus among many paleoanthropologists that the biological ancestors of today's humans evolved in Africa by the end of the Middle Pleistocene, almost 200000 years ago, and that these anatomically modern humans (AMH) then spread across the rest of the world during the Upper Pleistocene, replacing local populations. In western Eurasia, many believe AMH replaced the local Neanderthal populations with little or no inter-population genetic exchange [63, 69, 79]. This narrative model is based on inferences from the human fossil and archaeological records of Africa and western Eurasia, from the distribution patterns in genetic data from modern (i.e. 20th and 21st century) human populations, and from recent sequencing of DNA from several Eurasian Neanderthals [52] — although new genetic data raise questions about the previously supposed lack of genetic exchange between AMH and Neanderthals [46]. Here we develop a spatially-explicit, computational modeling environment to carry out a series of experiments that simulate population-scale interactions between AMH and Neanderthals in western Eurasia. We use this experimental protocol to examine the long-term effects of parameters that may have altered the character of that interaction, focusing especially on the biological impacts of different social and ecological behaviors among foragers. We then compare our results to the empirical record for this region.

1.1. *The experiments*

In our experiments, we modeled the long-term demographic consequences of several biobehavioral characteristics often mentioned in connection with the disappearance of Neanderthals in western Eurasia. Commonly, paleoanthropologists claim that behavioral differences between AMH and Neanderthals meant that individuals of

the latter population were less fit than those of the former. This means that Neanderthals had a lower reproductive potential than AMH either as the result of a relatively lower fertility or higher mortality. We examined the long-term consequences of interactions between two populations with the same fitness and with differential fertility or mortality.

Many paleoanthropologists also express the belief that there was no or virtually no genetic exchange between Neanderthal and AMH populations. This belief comes in part from the interpretation of limited genetic data [26] and from the apparent lack of AMH/Neanderthal hybrids (an issue treated in the experiments reported here). Biological mechanisms resulting in infertility separate most species and prevent successful interbreeding, but are unlikely in the case of Neanderthals and AMH. Recent sequencing of samples of Neanderthal DNA suggest a variety of possible dates for the last common ancestor of AMH populations living today and Neanderthals, but most fall between 700000 and 120000 years ago with a mean age of divergence around 300000–400000 years [43, 47, 52, 61, 70, 83]. Average rates for the evolution of hybrid inviability in mammals are between 2–4 million years, however, and several orders of magnitude greater than the oldest estimates for the age of biological divergence of AMH and Neanderthals [41, 43, 61]. In fact, the most recent genetic analyses of ancient DNA suggest that some (and possibly a significant) degree of interbreeding between AMH, Neanderthals, and other Upper Pleistocene hominin populations did occur [46, 89, 114] — and a very modest amount of gene flow can prevent biological speciation [44]. Even without biological infertility, however, other mechanisms also could have prevented or limited gene flow between AMH and Neanderthals. Social avoidance behavior is sometimes mentioned as preventing mating between AMH and Neanderthals [107]. Another mechanism is reduced fertility of AMH/Neanderthal hybrids [113]. We simulate both of these possibilities in our modeling environment. It is also possible, of course — though not discussed in the paleoanthropological literature — that AMH/Neanderthal hybrids could have been more fit than either parent population (i.e. hybrid vigor). We conducted experiments to track the long-term demographic consequences of all three possibilities in our modeling laboratory.

Finally, on the basis of archaeological (i.e. behavioral) data discussed in more detail below, there appears to be a shift in land-use and mobility patterns of hominins in western Eurasia during the Upper Pleistocene. The data suggest a shift towards increasingly logistical mobility strategies (LMS) that resulted in hominins periodically traveling longer distances for resource forays and, consequently, having opportunities to interact (socially and biologically) with other hominins at a greater distance than would be the case for foragers emphasizing a residential mobility strategy (RMS) within a more restricted home range. We model the demographic and biological consequences of shifting land-use strategies.

Of course, more than one of the behavioral patterns discussed above may have characterized hominin populations in western Eurasia at any given time. The experimental protocol permitted by our modeling laboratory approach allows us

Table 1. Simulation experiments in long-term hominin biocultural dynamics are reported here. Dark grey cells indicate experiments carried out and parameters controlled.

| | Fitness | | | | | |
	Equal	MM higher	NN higher	Hybrid higher	Hybrid lower	Assort. Mating
Assortative mating	■					
Mobility — RMS	■	■	■	■	■	■
Mobility — Intermediate	■					
Mobility — LMS	■	■	■	■		Equal fitness

to examine the effects of varying behavior simultaneously along more than one axis. The simulation experiments that we carried out are shown in Table 1 and the results are discussed below.

2. Methods

In order to examine the co-evolutionary impacts of behavioral change on Upper Pleistocene hominin demography, we employ an agent-based model or ABM (also called individual-based models in ecology) to represent biobehavioral dynamics in quantitative, algorithmic form. However, we are not trying to recreate the Upper Pleistocene world in digital form. We lack sufficiently detailed knowledge of Upper Pleistocene western Eurasia or the hominins who populated it to accomplish such a feat even if it were practical with currently available computer technology. Rather, we follow Bankes and others [8, 19] in treating ABM as an experimental laboratory in which we can carry out experiments to study the demographic consequences of particular hominin behaviors under a limited set of controlled conditions.

We created an ABM laboratory within the NetLogo 4.1 software package [117], a Java-based platform for creating and executing agent-based model simulations (Fig. 1). We have documented the ABM environment in detail, following the standardized ODD protocol [48, 85]. The ODD documentation and the NetLogo code of the ABM itself are available from the CoMSES Network Computational Model Library at http://www.openabm.org. We provide a brief overview of some of the most salient features of the ABM laboratory; additional information is available in the on-line Supplemental Information section.

The ABM is populated by agents that represent individuals possessing a simple genome, consisting of 10 allele pairs, and whose movement is constrained within a home range of a given radius. In the real world, each agent would be the
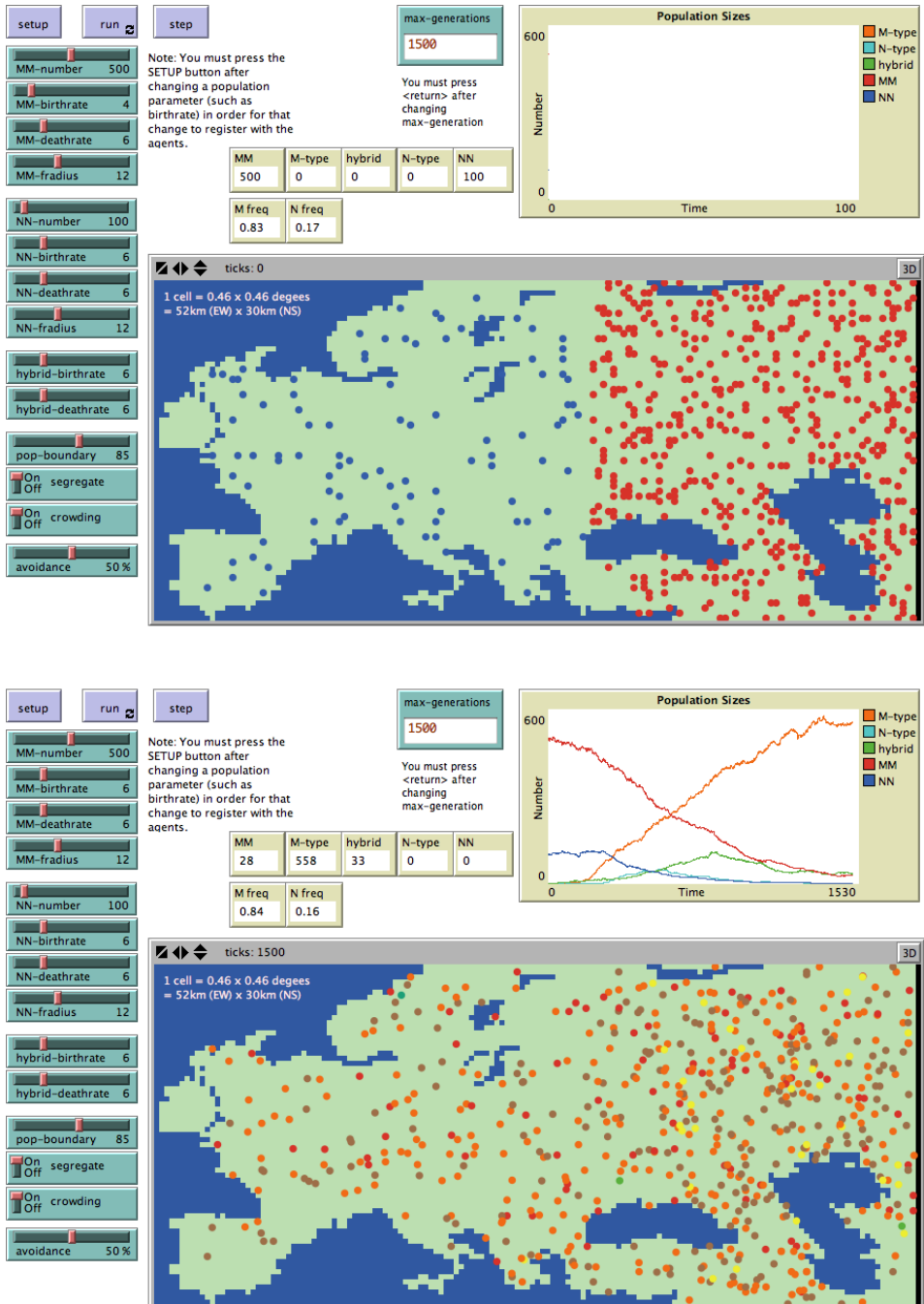
Fig. 1. NetLogo 4.1.1 modeling environment at the beginning (top) and the end (bottom) of a simulation experiment. Lines on graph indicate numbers of agents of each phenogenotype. Colors of agents indicate genotype: red is MM, blue is NN, and gradations between red and blue indicate the relative frequency of M and N alleles in each agent's genome.

representative of a local hunter-gather social group. The size of home ranges can be varied to simulate different mobility strategies (discussed more below). However, there is no directionality in agent movement or when offspring agents establish new home ranges; that is, agents do not migrate. The virtual world is configured to resemble a schematic map of Upper Pleistocene western Eurasia, to help visualize the spatial dynamics of AMH and Neanderthal interactions and demography at a continental scale. Nevertheless, confining agents to a real-world geography is not necessary for experiments on the effects of behavioral change on hominin demography and does not affect the working of the model or the simulation results.

Initially, all agents are assigned to one of two genetically distinct populations (e.g. Neanderthals and AMH) and are homozygous for different alleles at all loci (i.e. N_iN_i and M_iM_i, where i = locus). For the series of experiments reported here, all agents of population 1 are initially confined to western Eurasia (as with Neanderthals) while all agents of population 2 are initially placed in the "rest of the world" (representing AMH). Neanderthals are generally considered a morphologically distinct, semi-isolated population that was geographically limited to western Eurasia [52, 62]. Hence, we assume that the population of Neanderthals was considerably smaller than the total number of hominins in the rest of the world, and initiate our simulations with fewer Neanderthal agents than AMH agents. Neither the initial total number of agents nor the initial density of agents in the virtual landscape make much difference in the results. But, as we discuss below, the relative numbers of agents in each population at the start of a simulation do have a significant impact on the outcome in some experiments, but not in all.

Agent "fitness" is determined by birth and death rates which are set by the user and affect the chance that an agent will reproduce or die in each cycle of the simulation. A "crowding" option will temporarily increase the death rate when the number of agents exceeds the number of landscape patches in the virtual world, limiting run-away population increases. If an agent is allowed to reproduce, it will attempt to "mate" with another agent within its home range. If there are no other agents in the home range, the agent will simply clone itself to represent mating with an agent in its local group. The agent may or may not exhibit assortative mating preferences with the potential mate (i.e. if not cloned). With complete assortative mating, the chance that a pair will mate depends on the degree of similarity between their genomes. The strength of assortative mating can be varied from 100% to 0%; if the strength of assortative mating is 0%, then the degree of similarity is irrelevant for mating. When two different agents mate, their genomes combine through independent assortment to create the genome of their offspring. For tracking purposes, we classify agents into five "phenogenotypes". Agents with M and N gene frequencies of 1.0 are classed as MM and NN types respectively; agents with M or N gene frequencies of 0.25–0.75 are defined as "hybrids"; those with M or N gene frequencies between 0.76–0.99 are defined as "M-type" or "N-type" respectively.

As is the case in real life, and unlike a simple mathematical equation, any individual experimental run may not reach a permanent equilibrium state, unless one population goes to fixation. For this reason, we ran each simulation for a fixed number of iterations. Following empirical testing, we found that 1500 iterations were sufficient to clearly show trends in the data. Moreover, if modeling cycles are taken as analogous to human generations, 1500 iterations represent 30000–35000 years, approximately the period of overlap between Neanderthals and AMH in western Eurasia during OIS 3. Because each model run is unique, multiple runs with the same parameter settings can produce different results, and may or may not cluster around a particular outcome. Hence, we carried out 10 replications of a 1500-iteration run for each set of parameter settings. There are not yet generally accepted standards for evaluating the number of replications needed for this kind of modeling [8], but 10 replicates of each experiment provided clear trends for the study we present here.

3. Results

3.1. *Varying fitness*

The results of a series of experiments on the effects of varying relative fitness are shown in Fig. 2. For comparison, an initial experiment was conducted in which all agents in both initial populations and any hybrids from interbreeding have the same fitness — expressed as mortality and fertility rates (Fig. 2(a)). With no fitness differences, populations of MM (100% homozygous for M) and NN (100% homozygous for N) phenogenotypes simply fluctuate around their initial levels, and there are very few hybrids, M-type, or N-type agents. This can serve as a control model against which the effects of changing fitness parameters can be compared.

When MM agents have a fitness advantage (lower mortality), the number of MM agents is much higher after 1500 generations, as would be expected (Fig. 2(b)). Numbers of NN, N-type, and hybrid agents hover near 0. Interestingly, the numbers of M-type agents also increase greatly over the control model. These agents can be considered as representing small amounts of introgression of N genes. To the extent that phenotype is linked to genotype, these agents would be morphologically similar to MM agents. Hence, the total population after 1500 generations consists of agents who appear to be predominantly MM-like, with a variable, but small amount of N genes.

When NN agents have a fitness advantage (Fig. 2(c)), the results are largely the reverse of those produced with MM fitness advantage, but there are a few interesting differences. NN numbers are smaller and MM numbers are larger than in the opposite scenario, a result of the initial population differences (MM $\gg$ NN). Also the population of N-type agents remains low, again an outcome of the initial conditions.

The demographic results of hybrid disadvantage are seen in Fig. 2(d) and hybrid vigor in Fig. 2(e). When hybrids are less fit, MM and NN populations continue

(a) equal fitness

(b) MM More fit

(c) NN more fit
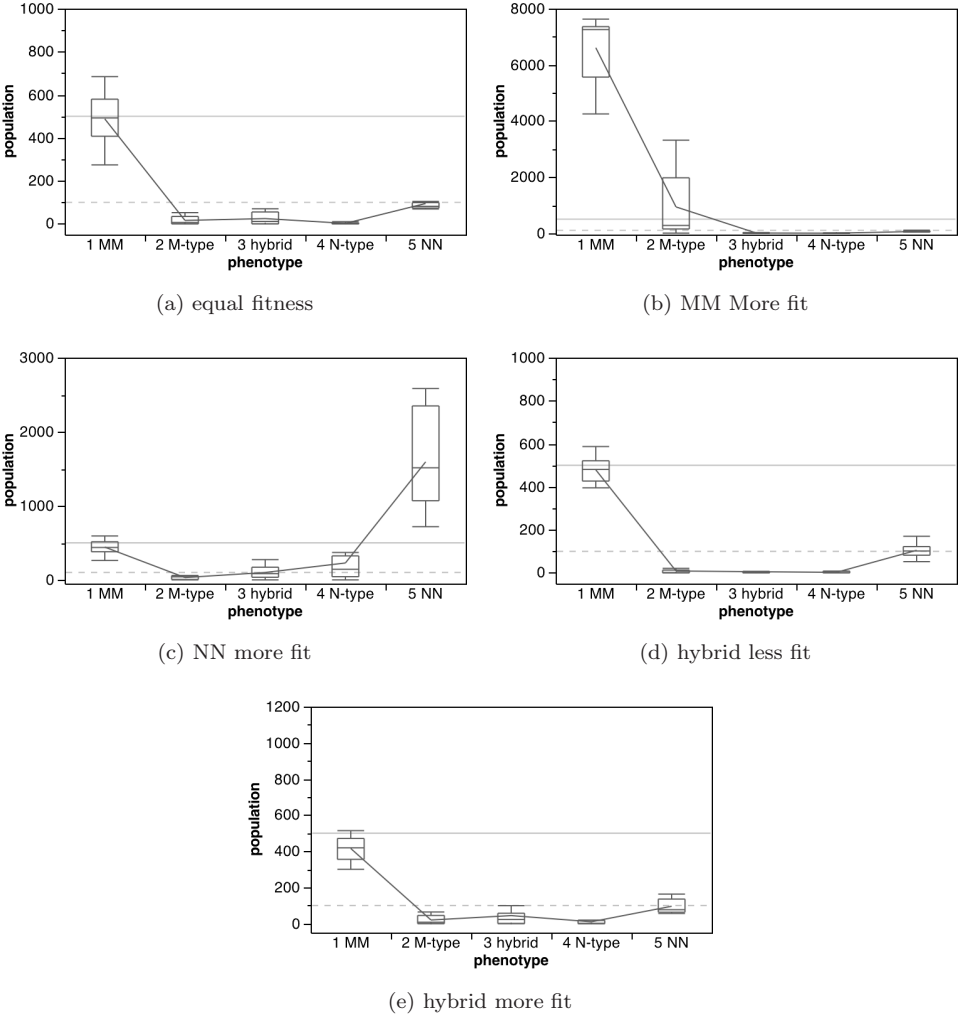
(d) hybrid less fit

(e) hybrid more fit

Fig. 2.   (a) Effects of fitness differences on phenogenotypes after 1500 generations. (b) MM agents have lower mortality; (c) NN agents have lower mortality; (d) hybrid agents have lower fertility; (e) hybrid agents have lower mortality. Baseline indicates RMS mobility. Solid lines indicate original MM population size. Dashed lines indicate original NN population size. Boxes show median and midspread; line connects mean.

to fluctuate around their original values, while all hybrids (including M-type and N-type) drop to near 0. Hybrid vigor has a slightly detrimental impact on MM population levels, but none on NN population levels. The total number of hybrid phenogenotypes remains low, however.

To the degree that it results in a combined population of MM and M-type agents only, the scenario represented by the MM fitness advantage experiment is consistent with the paleoanthropological record of western Eurasia by the end of OIS 3, while the others are not. On the other hand, the MM fitness advantage scenario results

in a population increase of many orders of magnitude in the numbers of MM/M-type agents, a phenomenon for which there is no evidence in this region until the mid-Holocene or later. This dramatic population increase, however, is in part a function of the design of the modeling environment. The reduced mortality causes the birthrate to exceed the deathrate, resulting in rapid population increase. Hence, it makes sense to consider the population make-up (all MM and M-type but no NN, N-type, or hybrids) but not the actual numbers in comparing the results of this experiment to the paleoanthropological record. The same holds true for other experiments described below.

3.2. *Socially-mediated controls on mating*

Figure 3 shows the results of experiments varying the degree to which socially-mediated mating controls, or assortative mating, could have affected genetic exchange between the two populations. The x-axis of each graph indicates the degree to which positive assortative mating was practiced. As noted above, with assortative mating = 0, the difference between the phenogenotypes of agents has no impact on whether they mate or not. If assortative mating = 100, agents have a 1.0 probability of mating with identical agents they encounter, a probability of 0.0 for mating with agents that are completely different (i.e. MM versus NN phenogenotypes), and a probability of mating that scales between 0 and 1 depending on the degree of difference between the agents.

Assortative mating has no effects on the numbers of MM and NN agents, because genetically identical agents always will mate and will produce identical offspring. Interestingly, assortative mating also has little effect on the long-term demographics of M-type, N-type, and hybrid agents. The populations of each these phenogenotypes after 1500 generations are approximately the same for all values of avoidance except for values at or above 90. That is, with even the smallest amount of interbreeding, there are agents who are sufficiently similar to permit additional gene flow. Over long time spans, the level of gene flow reaches an equilibrium value regardless of the strictness of avoidance behaviors. The only difference is that the equilibrium is reached sooner with less avoidance of different agent than it does with more avoidance. Thus, if Neanderthals and AMH could interbreed and if they came in contact with each other, it is likely that social proscriptions on mating with individuals who were visibly morphologically different is likely to have little to no impact of the rate of gene flow between the populations over long time spans.

3.3. *Land-use and mobility*

Figure 4 displays the results of varying the distance the agents traveled from their home range — for procuring resources, for example. If we again focus on population composition rather than total numbers of agents, increasing the mobility of the agents produces results very similar to that of giving MM individuals a fitness
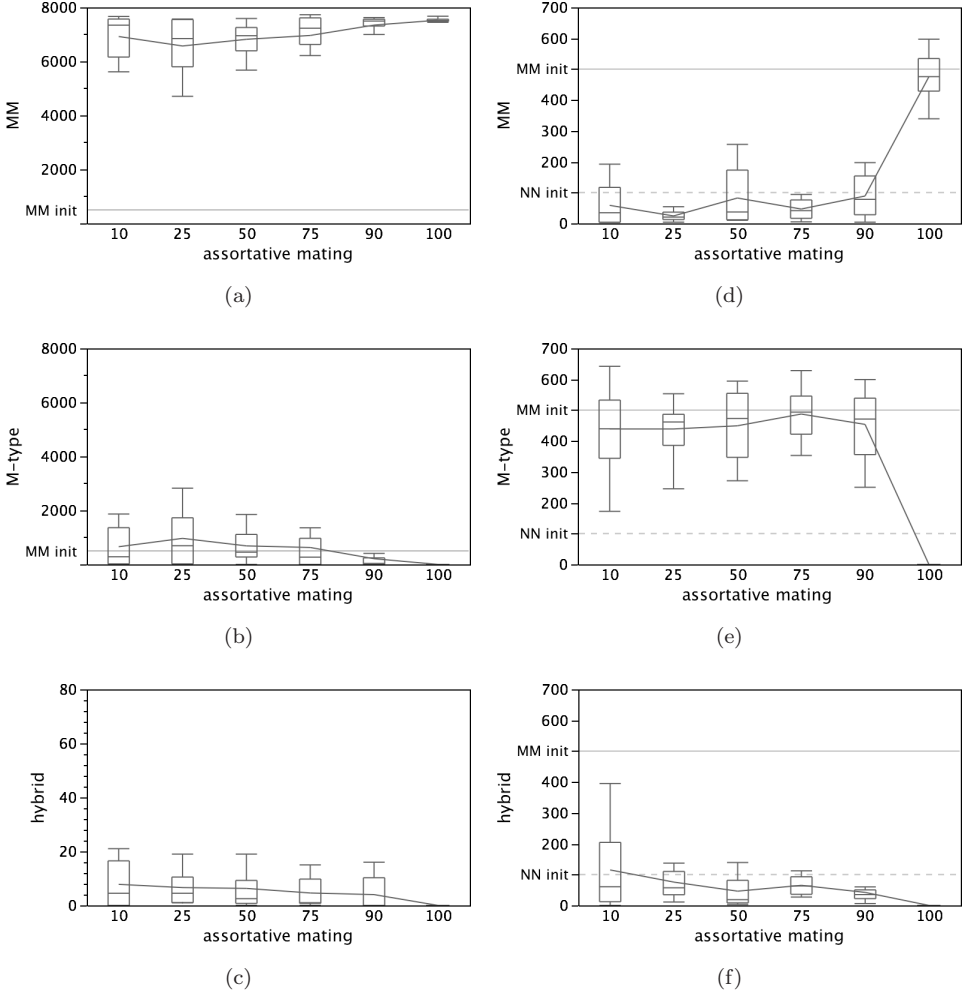
Fig. 3. Effects of different degrees of assortative mating on phenogenotypes after 1500 generations. For (a)–(c), MM have lower mortality and all agents have baseline RMS mobility. For (d)–(f), fitness of all agents is equal and all engage in LMS mobility. NN and N-type agents not shown, but show similar responses to assortative making as MM and M-type agents. Solid lines indicate original MM population size, dashed lines indicate original NN population size. Boxes show median and midspread; line connects mean. Note changing *y*-axis scales.

advantage: a final population composed of MM and M-type individuals, with virtually no NN or N-type individuals, and very few hybrids. The only difference is that when MM have a fitness advantage, MM individuals are more common than M-type individuals in the final population. With increasing mobility, M-type individuals are more common than MM individuals in the resulting population. Very similar results are obtained even when NN individuals have a fitness advantage over MM individuals (Fig. 4(f)).
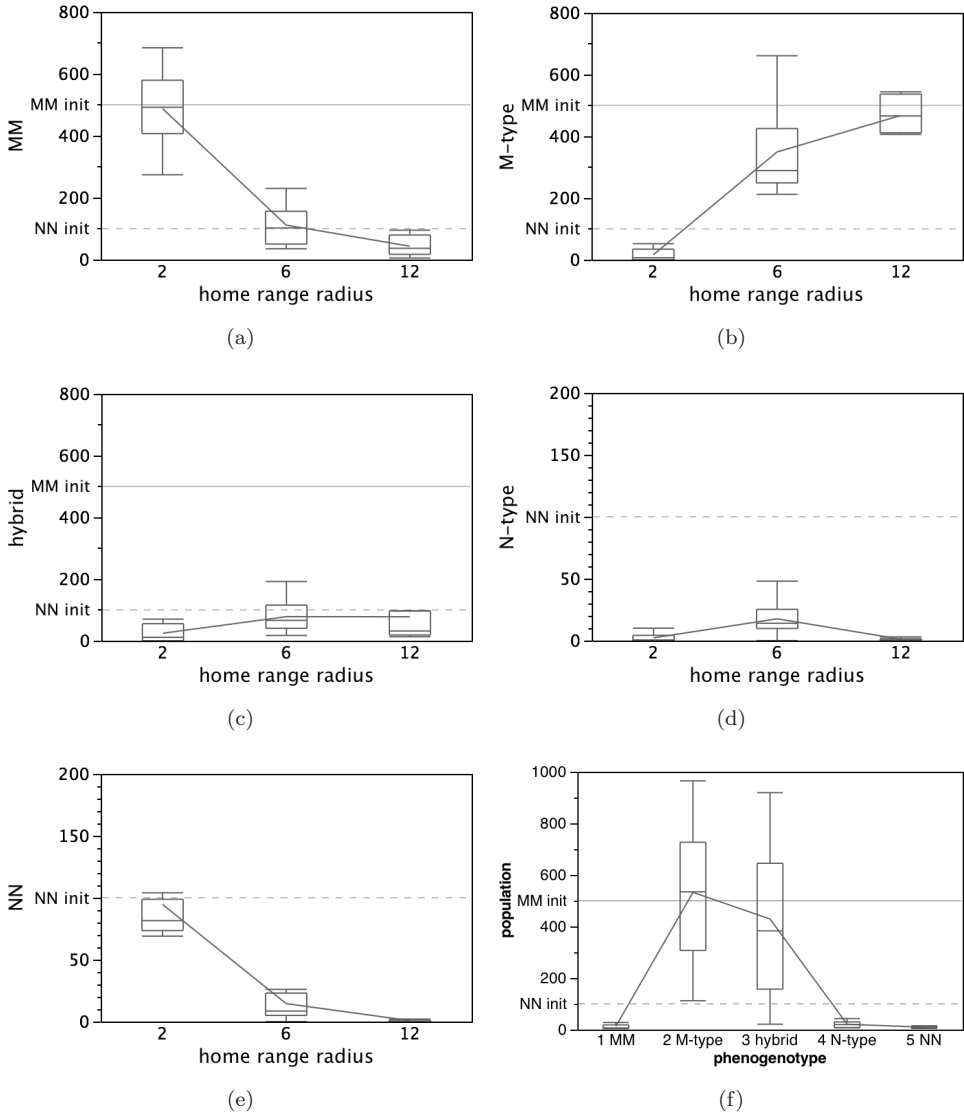
Fig. 4. Effects of increasing mobility on populations of each phenogenotype after 1500 generations. Fitness of all agents is equal for (a)–(e). For (f), NN is more fit (lower mortality) and all agents have home range radius of 12 cells. Boxes show median and midspread; line connects mean. Note changing y-axis scales for (d) and (e); x-axis for (a)–(e) in grid cells.

These results are a combined function of the different initial sizes of the two populations, coupled with increased chances for genetic interaction due to higher mobility. This phenomenon is well known in conservation biology where it is sometimes called extinction through hybridization and can have significant impacts on rare and endangered species [43, 118]. Biogeographical changes that increase interactions among members of different populations or even sister species (e.g. removal

of a geographic barrier or transportation by humans of one taxon into the range of another), commonly increase hybridization rates, leading to a rapid disappearance of the less numerous group as a recognizably distinct variant or species. Our modeling suggests that if populations are interfertile, even socially-mediated avoidance mechanisms cannot halt this process, unless such proscriptions are nearly 100% effective (Fig. 3).

In summary, our modeling experiments indicate two alternative processes that can lead to a high likelihood of extinction of a regionally distinctive and semi-isolated population like Neanderthals of western Eurasia: a significant fitness disadvantage relative to hominins in the rest of the world (i.e. AMH) or greater opportunities for social interaction and interbreeding due to increased mobility. In neither case does this extinction require a migration of AMH into Neanderthal territories or a diffusion-like wave of advance of "invading" hominins. In all experiments, the simulated populations interact only though the non-directional founding of new home-ranges by offspring of previous generations. We turn now to the archaeological and paleoanthropological records to compare the two models for Neanderthal extinction with the empirical record.

4. Testing Model Results

4.1. *Fitness in the paleoanthropological record*

Paleoanthropologists commonly assert that AMH had a significant fitness advantage over Neanderthals [9, 26, 69, 79]. Differences between AMH and Neanderthal material culture is often cited in support of this. Often, however, comparisons are between the artifacts in early Upper Pleistocene and late Upper Pleistocene assemblages that could be separated by over 50000 years of social and biological evolution [23, 106]. While these attest to dramatic changes in human cultural evolution over the course of the Upper Pleistocene, they are not helpful in identifying behaviors that could translate into fitness differences among contemporaneous Neanderthal and AMH hominins who interacted during OIS 3 in western Eurasia. Moreover, some of the purported differences in material culture have disappeared with the probable association of Neanderthals with the so-called "transitional" stone tool industries of Europe [92, 96, 106] and the discovery of beads and other items of personal adornment in assemblages that were almost certainly produced by European Neanderthals [34–36, 110]. Sometimes it seems like the primary evidence for AMH competitive advantage is the extinction of Neanderthals [69, 79].

AMH may have indeed had a fitness advantage over Neanderthals, but demonstrating this in a convincing way remains elusive — in a large part due to the inductive and narrative character of paleoanthropological model-building. Beyond speculative narratives, there has been virtually no theoretical and empirical research to robustly link Upper Pleistocene artifact assemblages with differences in hominin fertility or mortality. Our modeling experiments show how a fitness advantage alone is able to produce simulated results consistent with the human fossil record found

in western Eurasia at the end of the Pleistocene. The experiments also suggest that, unless there were fertility barriers or social barriers to mating between AMH and Neanderthals that were nearly 100% effective, there should be a small but still significant introgression of Neanderthal genetic material into the surviving population of western Eurasia. This is consistent with new genetic evidence comparing sequenced Neanderthal genomes to modern ones [46].

4.2. *Land-use and mobility*

Unlike competition and differential fitness, there is a robust body of theory and associated empirical data — developed over the past 30-plus years — that links the composition of stone artifact assemblages with forager technological and ecological behavior, including land-use and mobility. This research spans replicative and experimental studies [2, 25, 30, 64, 103, 116], ethnoarchaeological studies of stone tool users [45, 57, 60, 101, 102, 115], morphometrics of individual artifacts [5, 28, 42, 71, 78, 95, 99], and statistical analyses of whole assemblages [1, 7, 20, 31, 56, 86, 94, 100]. Because of its importance as a proxy for Pleistocene hominin behavior, we briefly review these relationships between stone technology and human ecology.

At the scale of human lifetimes, the ecology of hunter-gatherer land-use is complex and conditioned by a changing suite of environmental and social parameters [13, 16, 19, 32, 49, 50, 66, 67]. While most hunter-gatherers shift their residences with some regularity, there is variability in the frequency and distance of movement that is linked to the spatial and temporal distribution of important resources (especially food resources) and the ways in which these resources are harvested. Residential and logistical mobility strategies (RMS and LMS respectively) are defined as conceptual endpoints on this continuum of land-use that are useful for expressing variability in this important dimension of hunter-gatherer ecology [14, 50, 68, 81]. RMS refers to hunter-gatherers who move their camps to exploit resources available at different times and places, while LMS refers to a strategy in which camps are moved less often and groups of hunter-gatherers make targeted forays to acquire resources and return them to these "base camps". RMS and LMS tend to predominate under different environmental conditions and there is a general, though not exclusive, tendency for logistical resource forays to cover greater distances than residential hunter-gatherers moving from one resource patch to the next [15, 16, 50, 66, 67].

When moving across the landscape to collect resources or to relocate a residence, a hunter-gatherer uses more energy to carry stone artifacts than an equivalent volume of food, water, or infants. Yet chipped stone's ubiquity in the archaeological record attests to its importance for human survival — for procuring and processing resources, and for crafting other items of technology. Importantly, even though stone is durable, lithic artifacts commonly have use-lives on the order of hours [6, 42, 45]; stone tool edges dull rapidly, and their rejuvenation through flaking (i.e. retouch)

rapidly reduces tools to an unusable size [10, 29, 42]. Moreover, making lithic arti-
facts rapidly produces a large quantity of flakes, fragments, and debris, only some
of which are useful [1, 4, 76, 77, 82]. As a result, hunter-gatherer mobility strategies
can affect the nature of stone artifact assemblages found in the paleoanthropolog-
ical record. For hunter-gatherers emphasizing RMS, regular movement of residen-
tial camps puts a premium on portability, creating an "effective scarcity" of lithic
materials [94, 95], regardless of the geographic distribution of useable stone on the
landscape. This encourages RMS hunter-gatherers to extend the short use-lives of
their stone artifacts by resharpening dulled edges, allowing them to minimize the
amount of heavy stone that they need to carry. LMS organized hunter-gatherers,
however, can stockpile stone at base camps where they are transiently sedentary
between resource forays [72]. Additionally, because lithic technology rapidly gen-
erates large quantities of products, and because logistical hunter-gatherers at base
camps depend less on extending the artifact's lifespan through retouch, LMS base
camps should be characterized by abundant lithic assemblages with lower retouch
frequencies (i.e. fewer retouched artifacts).

At the resolution of daily activities of actual forager groups many parameters
can affect the production, use, and discard of stone artifacts — ranging from local
availability of stone to the different uses of stone artifacts — and these can vary
according to the geographical locations of camps, the season of the year, and access
to non-stone resources (e.g. food plants and animals). However, artifact assem-
blages at most Pleistocene hominin sites are time-averaged palimpsests of trash
from repeated occupations by hunter-gatherer groups that accumulated over gener-
ations, rather than residues of discrete encampments [12, 37, 94]. We have suggested
previously that the relative frequency of retouch in these palimpsests provides a
time-averaged proxy signal for prehistoric mobility strategies of Pleistocene hunter-
gathers [11, 94, 95, 97, 112]. If this is correct, given the model we outline above for
the relationships between mobility and stone technology, there should be a negative
correlation between retouch relative frequency and artifact density in lithic assem-
blages from these sites. That is, the more that refuse from logistical base camps con-
tributed to an assemblage, the greater the volumetric density of lithic material and
the lower the retouch frequency. Conversely, the more residentially mobile hunter-
gatherers contributed lithic trash to an assemblage, the lower its density and higher
its retouch frequency. We have found repeatedly that assemblages across southern
Europe match this prediction [11, 94, 95, 97, 112] and others have replicated these
results independently [22, 73, 98].

While both retouch frequency and artifact density can serve as proxies for human
land-use strategies, lithic density can vary considerably due to sediment deposition
rates at different sites and even over time within individual sites [11, 52, 94, 97].
The relative frequency of retouched pieces out of all artifacts in a lithic assemblage,
in contrast, is a normalized measure much less affected by differences in deposi-
tional environments or assemblage size. Importantly, retouch frequency is commonly
reported for Paleolithic assemblages, making it widely available for comparative
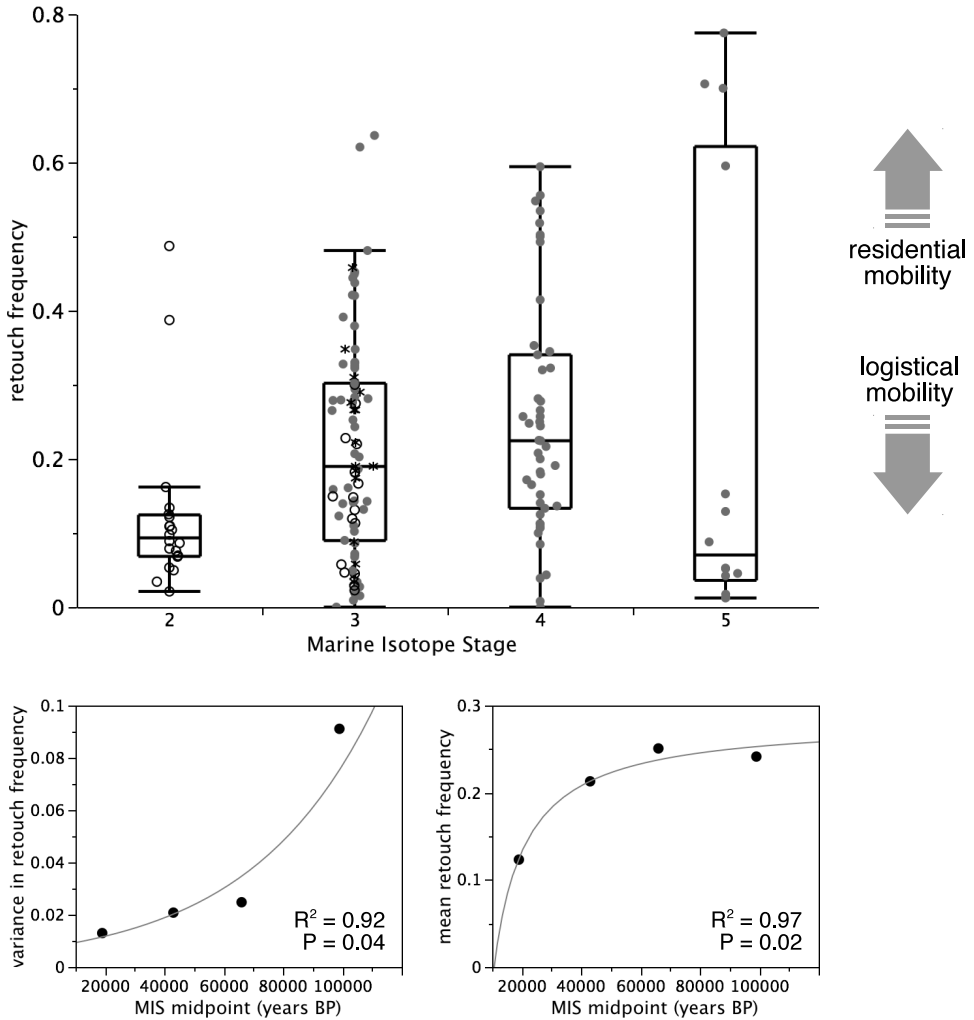
Fig. 5. Top graph shows frequency of retouched artifacts in 167 Upper Pleistocene lithic assemblages from western Eurasia [11, 24, 91, 94, data originally published in 95, 97, 112]. Solid grey circles are Middle Paleolithic artifact assemblages (probably made by Neanderthals), black asterisks are Transitional Industry assemblages (probably made by Neanderthals), and open circles are Upper Paleolithic assemblages (probably made by AMH). Bottom graphs do not indicate causal relationships but simply distill the non-random time trends in mean and variance of retouch frequency shown in the box plot.

studies at large spatial and temporal scales. Hence, we use retouch frequency here as a proxy measure of Upper Pleistocene land-use strategies.

Figure 5 shows retouch frequency for 167 Upper Pleistocene assemblages from western Eurasia. Temporally, the assemblages span nearly the entirety of the Upper Pleistocene, from the last Interglacial (OIS 5) through the end of the Pleistocene (OIS 2). Geographically, these assemblages are from sites distributed from Gibraltar

to the Levant. Three time-trends apparent in Fig. 5 are particularly relevant for the hominin demography models presented above. Firstly, using the frequency of retouched pieces in stone artifact assemblages as a proxy, the variability in mobility strategies practiced in western Eurasia declines from OIS 5 through OIS 2. Secondly, the reduction in variability in mobility strategies is due to an increasing focus on LMS over time. Thirdly, for the time period in which both AMH and Neanderthals were making, using and discarding stone artifacts in western Eurasia (i.e. OIS 3), both populations display similar diversity and time trends in mobility strategies.

These proxy data indicate that during the Upper Pleistocene, western Eurasian hominins became increasingly reliant on LMS land-use. This in turn, led to hominins traveling longer distances and offered increased opportunities for social and biological interaction among neighboring groups. Under these conditions, our computational model experiments predict that it is likely that Neanderthals would go extinct as a recognizably distinct population, regardless of any social barriers to mating between individuals who appeared different. Moreover, if there were fewer Neanderthals in western Eurasia than hominins in the rest of the world (a reasonable, though untested assumption), extinction is likely even if Neanderthals were better adapted to western Eurasian environments than AMH (i.e. were more fit).

4.3. *Site distributions and human ecology*

Spatial-temporal distributions of hominin fossils and artifact assemblages during the Upper Pleistocene provides additional evidence pertinent to testing these alternative extinction models. Neanderthals and AMH co-occur in western Eurasia during OIS 3, a time of increasingly unstable and rapidly cooling climate [52, 92, 104]. During OIS 3, Neanderthals are found throughout southern Europe, while contemporaneous specimens of AMH are found initially in Central/Eastern Europe [3, 39, 40, 109]. At that time, southern Europe was the most mesic part of the subcontinent, with the most diverse and easily procured food resources, and hence the most desirable part of Europe from a hunter-gatherer perspective [51, 111]. AMH, on the other hand, initially were restricted to the expanding periglacial steppe and adjacent areas, a region that must have been especially challenging ecologically for hunter-gatherers originating in Africa [59].

Competitive exclusion of newly arrived hunter-gatherers to the less desirable margins of already inhabited landscapes is not surprising, and is documented in the later archaeological and historic records [38]. If all populations have similar capabilities, those with a "home-field advantage" of better local knowledge and behaviors adapted to local conditions and resources will be able to outcompete newcomers. If AMH were populations expanding from Africa into Eurasia and had a significant inherent fitness advantage over Neanderthals, they should have been able to push Neanderthals into the marginal and less desirable habitats of the subcontinent, much as agriculturalists have geographically marginalized remaining hunter-gather populations in the Holocene. However, the available distributional

data suggests the opposite — that Neanderthals restricted AMH to the ecological margins of western Eurasia for millennia.

This evidence remains indirect and circumstantial, but argues against AMH having a significant inherent fitness advantage over Neanderthals. On the other hand, it is not problematic for a shifting mobility model of extinction. Changing land-use patterns in response to Pleistocene environmental changes would have greatly increased the likelihood of Neanderthal extinction regardless of whether their local knowledge and skills initially gave them an advantage over newcomers.

5. Concluding Thoughts

The Upper Pleistocene was the critical time for the coalescence of human behavioral modernity, the period in which culture became the fundamental evolutionary force for complex behavior in our species [53, 55]. At some time, probably in the Upper Pleistocene, the number of interacting human social learners passed a threshold that permitted the emergence of culture as an inheritance system of socially-transmitted, cumulative knowledge that drives complex human behaviors and social interactions [18, 65, 87]. Culture, as a possibly uniquely human form of social learning, in turn allowed humans to adapt rapidly through culturally mediated behaviors to rapid environmental change. Possibly for the first time, humans continued to occupy western Eurasia, and even thrived, throughout the glacial period marked by the Upper Pleistocene. Neanderthals appear to exhibit the same ability to respond culturally and behaviorally to the rapid environmental changes that mark OIS 3 in western Eurasia [93]. Certainly they inhabited a broad swath of this region as the climate shifted into glacial mode from late OIS 5 through OIS 3. Neanderthal culturally-mediated behavioral responses to environmental change in this region show up in increasingly diverse lithic technology — the so-called "transitional" industries of OIS 3 [23, 33, 96, 106] — and in the shifting land-use strategies that we document above.

But these successful cultural responses to environmental change also had biological, and probably social, consequences as previously isolated Neanderthal populations came into increasing contact with the wider world. The most significant of these consequences was the disappearance of Neanderthals biologically and culturally as a distinctive, regional population of western Eurasia. In a paper that critically reviews evidence for the interaction of Neanderthals and AMH in western Eurasia during the Upper Pleistocene, Paul Mellars [80] voices a question that has been central to ongoing debate over the course of human evolutionary history in this region. Noting that Neanderthals successfully occupied temperate and glacial western Eurasia for at least 200000 years while AMH were recent immigrants from sub-Saharan Africa, he asks "... if the European Neanderthals were so cognitively advanced and had developed most if not all of the elements of characteristically "modern" culture and cognition, why did they succumb so rapidly to a biologically

and environmentally less well-adapted species within a space of, at most, a few thousand years?"

The approach we advocate here, developing and testing theory-based formal models, is in its infancy. We can neither observe nor accurately infer the dynamic interactions of hominin biology and culture in the distant past. But we can model these dynamics in explicit and transparent ways that can be evaluated against the empirical record. This allows us to develop and improve on a cumulative body of knowledge, and can lead to new insights about about human biocultural evolution. Hopefully, this work will inspire others to replicate, improve on our models or develop ones that better match the empirical record. We also hope it will encourage new, theory driven approaches to the record. (e.g. recent work suggest methods that may lead to better information about relative fitness [58, 105]). Based on the modeling experiments and empirical evaluation of the seemingly counter-intuitive results, we answer the question that Mellars poses by suggesting that Neanderthals disappeared from the paleoanthropological record precisely *because* they "... had developed most if not all of the elements of characteristically "modern" culture and cognition ... " [80], not inspite of it. But like their DNA, a small amount of which seems to live on in modern humans, perhaps aspects of Neanderthal cultural knowledge also spread to those subtropical humans who took their place, and helped them to survive and thrive in Pleistocene western Eurasia after Neanderthals disappeared.

Acknowledgments

References

[1] Ahler, S. A., Mass analysis of flaking debris: studying the forest rather than the tree, in *Alternative Approaches to Lithic Analysis*, Henry, D. O. and Odell, G. H. (eds.) (Archaeological Papers of the American Anthropological Association Number 1, 1989), pp. 85–118.

[2] Amick, D. and Mauldin, R. P. (eds.), *Experiments in Lithic Technology* (BAR International Series 528, Oxford, 1989).

[3] van Andel, T. H., Davies, S. W. and Weninger, B., The human presence in Europe during the last glacial period I: human migrations and the changing climate, in *Neanderthals and Modern Humans in the European Landscape During the Last Glaciation*, van Andel, T. H. and Davies, S. W. (eds.) (McDonald Institute for Archaeological Research, Cambridge, 2003), pp. 31–56.

[4] Andrefsky, W., *Lithic Debitage: Context, Form, Meaning* (University of Utah Press, Salt Lake City, 2001).

[5] Andrefsky, W., *Lithic Technology: Measures of Production, Use and Curation*, 1st edn. (Cambridge University Press, Cambridge, 2008).

[6] Bamforth, D. B., Technological efficiency and tool curation, *Am. Antiquity* **51** (1986) 38–50.

[7] Bamforth, D. B. and Becker, M. S., Core/biface ratios, mobility, refitting, and artifact use-lives: A Paleoindian example, *Plains Anthropol.* **45** (2000) 273–290.

[8] Bankes, S. C., Lempert, R. and Popper, S., Making computational social science effective: Epistemology, methodology, and technology, *Soc. Sci. Comput. Rev.* **20** (2002) 377–388.

[9] Banks, W. E., d' Errico, F., Peterson, A. T., Kageyama, M., Sima, A. and Sánchez-Goñi, M.-F., Neanderthal extinction by competitive exclusion, *PLoS ONE* **3** (2008) e3972.

[10] Barton, C. M., Beyond style and function: A view from the Middle Paleolithic, *Am. Anthropol.* **92** (1990) 57–72.

[11] Barton, C. M., Looking back from the world's end: Paleolithic settlement and mobility at Gibraltar, in *Las Culturas Del Pleistoceno Superior En Andalucía*, Sanchidrián Torti, J. L. and Simón Vallejo, M. D. (eds.) (Patronato de la Cueva de Nerja, Nerja, 1998), pp. 13–23.

[12] Barton, C. M. and Clark, G. A., Cultural and natural formation processes in late Quaternary cave and rockshelter sites of western Europe and the Near East, in *Formation Processes in Archaeological Context*, Goldberg, P., Nash, D. T. and Petraglia, M. D. (eds.) (Prehistory Press, Madison, WI., 1993), pp. 33–52.

[13] Bettinger, R. L., *Hunter-Gatherers: Archaeological and Evolutionary Theory* (Plenum Press, New York, 1991).

[14] Binford, L. R., Organization and formation processes: looking at curated technologies, *J. Anthropol. Res.* **35** (1979) 255–273.

[15] Binford, L. R., Willow smoke and dogs' tails: Hunter-gatherer settlement systems and archaeological site formation, *Am. Antiquity* **45** (1980) 4–20.

[16] Binford, L. R., *Constructing Frames of Reference: An Analytical Method for Archaeological Theory Building Using Hunter-Gatherer and Environmental Data Sets*, 1st edn. (University of California Press, Berkeley, 2001).

[17] Bowles, S. and Gintis, H., The origins of human cooperation, in *Genetic and Cultural Evolution of Cooperation*, Hammerstein, P. (ed.) (The MIT Press, Cambridge, MA, 2003), pp. 429–443.

[18] Boyd, R. and Richerson, P. J., Why culture is common, but cultural evolution is rare, in *Proceedings of the British Academy* (1996), pp. 77–94.

[19] Brantingham, P. J., Measuring forager mobility, *Curr. Anthropol.* **47** (2006) 435–459.

[20] Carr, P. J. and Bradbury, A. P., Flake debris analysis, levels of production and the organization of technology, in *Lithic Debitage: Context, Form, Meaning*, Andrefsky Jr., W. (ed.) (University of Utah Press, Salt Lake City, 2001), pp. 126–146.

[21] Christiansen, M. H. and Kirby, S., Language evolution: Consensus and controversies, *Trends Cogn. Sci.* **7** (2003) 300–307.

[22] Clark, A. E., Changes in occupation intensity during the lower and middle Paleolithic at Tabun cave, Israel, Master's Paper (University of Arizona, 2008).

[23] Clark, G. A. and Riel-Salvatore, J., What's in a name? Observations on the compositional integrity of the Aurignacian, in *The Mediterranean from 50000 to 25000*

BP: Turning Points and New Directions, Camps, M. and Szmidt, C. (eds.) (Oxbow Books, Oxford, 2009), pp. 323–338.

[24] Coinman, N. R. (ed.), *The Archaeology of the Wadi al-Hasa, West-Central Jordan, Vol. 2: Excavations at Middle, Upper and Epipaleolithic Sites in the Hasa* (Arizona State University Anthropological Research Papers, Tempe, 2000).

[25] Cotterell, B. and Kamminga, J., The formation of flakes, *Am. Antiquity* **52** (1987) 675–708.

[26] Currat, M. and Excoffier, L., Modern humans did not admix with Neanderthals during their range expansion into Europe, *PLoS Biol.* **2** (2004) e421.

[27] Deacon, T. W., Evolutionary perspectives on language and brain plasticity, *J. Commun. Disord.* **33** (2000) 273–291.

[28] Dibble, H. L., The interpretation of Middle Paleolithic scraper morphology, *Am. Antiquity* **52** (1987) 109–117.

[29] Dibble, H. L., Middle Paleolithic scraper reduction: background, clarification and review of the evidence to date, *J. Archaeol. Method Th.* **2** (1995) 299–368.

[30] Dibble, H. L. and Rezek, Z., Introducing a new experimental design for controlled studies of flake formation: results for exterior platform angle, platform depth, angle of blow, velocity and force, *J. Archaeol. Sci.* **36** (2009) 1945–1954.

[31] Douglas, M. J., Holdaway, S. J., Fanning, P. C. and Shiner, J. I., An assessment and archaeological application of cortex measurement in lithic assemblages, *Am. Antiquity* **73** (2008) 513.

[32] Eder, J. F., The impact of subsistence change on mobility and settlement pattern in a tropical forest foraging economy: Some implications for archeology, *Am. Anthropol.* **86** (1984) 837–853.

[33] d' Errico, F., The invisible frontier. A multiple species model for the origin of behavioral modernity, *Evol. Anthropol.* **12** (2003) 188–202.

[34] d' Errico, F., The origin of humanity and modern cultures: archaeology's view, *Diogenes* **54** (2007) 122–133.

[35] d' Errico, F., Henshilwood, C., Lawson, G., Vanhaeren, M., Tillier, A.-M., Soressi, M. *et al.*, Archaeological evidence for the emergence of language, symbolism and music — an alternative multidisciplinary perspective, *J. World Prehist.* **17** (2003) 1–70.

[36] d' Errico, F., Vanhaeren, M., Barton, R. N. E., Bouzouggar, A., Mienis, H., Richter, D. *et al.*, Additional evidence on the use of personal ornaments in the Middle Paleolithic of North Africa, *Proceedings of the National Academy of Sciences* **106** (2009) 16051–16056.

[37] Farrand, W. R., Archaeological sediments in caves and rockshelters, in *Sediments in Archaelogical Context*, Stein, J. K. and Farrand, W. R. (eds.) (University of Utah Press, Salt Lake City, 2001), pp. 29–66.

[38] Fiedel, S. J., Rapid migrations by Arctic hunting peoples: Clovis and Thule, in *The Settlement of the American Continents: A Multidisciplinary Approach to Human Biogrography*, Barton, C. M., Clark, G. A., Yesner, D. R. and Pearson, G. (eds.) (University of Ariz. Press, Tucson, 2004), pp. 79–84.

[39] Finlayson, C. and Carrión, J. S., Rapid ecological turnover and its impact on Neanderthal and other human populations, *Trends Ecol. & Evol.* **22** (2007) 213–222.

[40] Finlayson, C., Giles Pacheco, F., Rodriguez-Vidal, J., Fa, D. A., Maria Gutierrez Lopez, J., Santiago Perez, A. *et al.*, Late survival of Neanderthals at the southernmost extreme of Europe, *Nature* **443** (2006) 850–853.

[41] Fitzpatrick, B. M., Rates of evolution of hybrid inviability in birds and mammals, *Evolution* **58** (2004) 1865–1870.

[42] Frison, G. C., A functional analysis of certain chipped stone tools, *Am. Antiquity* **33** (1968) 149–155.

[43] Garrigan, D. and Kingan, S. B., Archaic human admixture: a view from the genome, *Curr. Anthropol.* **48** (2007) 895–902.

[44] Gillespie, J. H., *Population Genetics: A Concise Guide* (Johns Hopkins University Press, 2004).

[45] Gould, R. A. K., Koster, D. A. and Sontz, A. H. L., The lithic assemblage of the western desert aborigines of Australia, *Am. Antiquity* **36** (1971) 149–168.

[46] Green, R. E., Krause, J., Briggs, A. W., Maricic, T., Stenzel, U., Kircher, M. *et al.*, A draft sequence of the Neandertal genome, *Science* **328** (2010) 710–722.

[47] Green, R. E., Krause, J., Ptak, S. E., Briggs, A. W., Ronan, M. T., Simons, J. F. *et al.*, Analysis of one million base pairs of Neanderthal DNA, *Nature* **444** (2006) 330–336.

[48] Grimm, V., Berger, U., Bastiansen, F., Eliassen, S., Ginot, V., Giske, J. *et al.*, A standard protocol for describing individual-based and agent-based models, *Ecol. Model.* **198** (2006) 115–126.

[49] Grove, M., Hunter-gatherer movement patterns: Causes and constraints, *J. Anthropol. Archaeol.* **28** (2009) 222–233.

[50] Grove, M., Logistical mobility reduces subsistence risk in hunting economies, *J. Archaeol. Sci.* **37** (2010) 1913–1921.

[51] Hardy, B. L., Climatic variability and plant food distribution in Pleistocene Europe: implications for Neanderthal diet and subsistence, *Quaternary Sci. Rev.* **29** (2010) 662–679.

[52] Harvati, K., Neanderthals and their contemporaries, in *Handbook of Paleoanthropology*, 2007), pp. 1717–1748.

[53] Henrich, J. and McElreath, R., The evolution of cultural evolution, *Evolutionary Anthropology: Issues, News and Reviews* **12** (2003) 123–135.

[54] Henshilwood, C. S. and Marean, C. W., The origin of modern human behavior, *Curr. Anthropol.* **44** (2003).

[55] Hill, K., Barton, C. M. and Hurtado, A. M., The emergence of human uniqueness: Characters underlying behavioral modernity, *Evolutionary Anthropology: Issues, News and Reviews* **18** (2009) 187–200.

[56] Hiscock, P., Quantifying the size of artefact assemblages, *J. Archaeol. Sci.* **29** (2002) 251–258.

[57] Hiscock, P., Slippery and billy: Intention, selection and equifinality in lithic artefacts, *Camb. Archaeol. J.* **14** (2004) 71–77.

[58] Hockett, B. and Haws, J. A., Nutritional ecology and the human demography of Neandertal extinction, *Quatern. Int.* **137** (2005) 21–34.

[59] Hoffecker, J. F., *A Prehistory of the North* (Rutgers University Press, 2005).

[60] Holdaway, S. and Douglass, M., A twenty-first century archaeology of stone artifacts, *J. Archaeol. Method Th.* (2011).

[61] Holliday, T., Neanderthals and modern humans: an example of a mammalian syngameon? in *Neanderthals Revisited: New Approaches and Perspectives*, (2006), pp. 281–297.

[62] Hublin, J.-J. The origin of Neandertals, *Proceedings of the National Academy of Sciences* **106** (2009) 16022–16027.

[63] Hublin, J.-J. and Bailey, S. E., Revisiting the last Neandertals, in *When Neanderthals and Modern Humans Met*, Conard, N. J. (ed.) (Kerns Verlag, Tübingen, 2006), pp. 105–128.

[64] Johnson, L. L., A history of flint-knapping experimentation 1838–1976, *Curr. Anthropol.* **19** (1978) 337–372.

[65] Kameda, T. and Nakanishi, D., Does social/cultural learning increase human adaptability? Rogers' question revisited, *Evol. Hum. Behav.* **24** (2003) 242–260.

[66] Kelly, R. L., Hunter-gatherer mobility strategies, *J. Anthropol. Res.* **39** (1983) 277–306.

[67] Kelly, R. L., *The Foraging Spectrum: Diversity in Hunter-Gatherer Lifeways* (Smithsonian Institution Press, Washington, DC, 1995).

[68] Kim, J., Land-use conflict and the rate of the transition to agricultural economy: A comparative study of southern scandinavia and central-western Korea, *J. Archaeol. Method Th.* **10** (2003) 277–321.

[69] Klein, R. G., Paleoanthropology: Whither the Neanderthals?, *Science* **299** (2003) 1525–1527.

[70] Krau, J., Lalueza-Fox, C., Orlando, L., Enard, W., Green, R. E., Burbano, H. A. *et al.*, The derived FOXP2 variant of modern humans was shared with Neandertals, *Curr. Biol.* **17** (2007) 1908–1912.

[71] Kuhn, S. L., Unpacking reduction: Lithic raw-material economy in the Mousterian of West-Central Italy, *J. Anthropol. Archaeol.* **10** (1991) 76–106.

[72] Kuhn, S. L., On planning and curated technologies in the Middle Paleolithic, *J. Anthropol. Res.* **48** (1992) 185–214.

[73] Kuhn, S. L. and Johnson, A. L., Middle paleolithic assemblage formation at riparo mochi, in *Processual Archaeology: Exploring Analytical Strategies, Frames of Reference and Culture Process* (Greenwood Publishing Group, Westport, CT, 2004), pp. 31–60.

[74] Laland, K. N., Odling-Smee, F. J. and Feldman, M. W., Cultural niche construction and human evolution, *J. Evol. Biol.* **14** (2001) 22–33.

[75] Laland, K. N., Odling-Smee, F. J. and Myles, S., How culture shaped the human genome: bringing genetics and the human sciences together, *Nat. Rev. Genet.* **11** (2010) 137–148.

[76] Magne, M. P. and Pokotylo, D., A pilot study in bifacial lithic reduction sequences, *Lithic Technology* **10** (1981) 34–47.

[77] Mauldin, R. P. and Amick, D. S., Investigating patterning in debitage from experimental bifacial core reduction, in *Experiments in Lithic Technology*, Amick, D. S. and Mauldin, R. P. (eds.) (BAR, Oxford., 1989), pp. 67–88.

[78] McPherron, S. P., Handaxes as a measure of the mental capabilities of early Hominids, *J. Archaeol. Sci.* **27** (2000) 655–663.

[79] Mellars, P., Neanderthals and the modern human colonization of Europe, *Nature* **432** (2004) 461–465.

[80] Mellars, P., The impossible coincidence: a single-species model for the origins of modern human behavior in Europe, *Evol. Anthropol.* **14** (2005) 12–27.

[81] Nelson, M. C., The study of technological organization, *J. Archaeol. Method Th.* **3** (1991) 57–100.

[82] Newcomer, M. H., Some quantitative experiments in handaxe manufacture, *World Archaeol.* **3** (1971) 85–94.

[83] Noonan, J. P., Coop, G., Kudaravalli, S., Smith, D., Krause, J., Alessi, J. *et al.*, Sequencing and Analysis of Neanderthal Genomic DNA, *Science* **314** (2006) 1113–1118.

[84] Pinker, S., Language as an adaptation to the cognitive niche, in *Language Evolution*, Christiansen, M. H. and Kirby, S. (eds.) (Oxford U Press, New York, 2003), pp. 16–37.

[85] Polhill, J. G., Parker, D. C., Brown, D. G. and Grimm, V., Using the ODD protocol for describing three agent-based social simulation models of land use change, *Journal of Artificial Societies and Social Simulation* **11** (2008) 3.

[86] Popescu, G., Estimating the size of lithic artifact assemblages: a view from the Southern Carpathians Middle Paleolithic, *Studii De Preistorie* **5** (2008) 37–49.

[87] Powell, A., Shennan, S. and Thomas, M. G., Late Pleistocene demography and the appearance of modern human behavior, *Science* **324** (2009) 1298–1301.

[88] Premo, L. S. and Hublin, J.-J., Culture, population structure and low genetic diversity in Pleistocene hominins, *Proceedings of the National Academy of Sciences* **106** (2009) 33–37.

[89] Reich, D., Green, R. E., Kircher, M., Krause, J., Patterson, N., Durand, E. Y. *et al.*, Genetic history of an archaic hominin group from Denisova Cave in Siberia, *Nature* **468** (2010) 1053–1060.

[90] Richerson, P. J., Boyd, R. and Henrich, J., Colloquium paper: Gene-culture coevolution in the age of genomics, *Proceedings of the National Academy of Sciences* **107** (2010) 8985–8992.

[91] Riel-Salvatore, J., The Uluzzian and the Middle-Upper Paleolithic transition in southern Italy, PhD Dissertation, Arizona State University (2007).

[92] Riel-Salvatore, J., What is a "transitional" industry? The Uluzzian of southern Italy as a case study, in *Sourcebook of Paleolithic Transitions: Methods, Theories and Interpretations*, Camps, M. and Chauhan, P. (eds.) (Springer, New York, 2009), pp. 377–396.

[93] Riel-Salvatore, J., A Niche Construction Perspective on the Middle–Upper Paleolithic Transition in Italy, *J. Archaeol. Method Th.* **17** (2010) 323–355.

[94] Riel-Salvatore, J. and Barton, C. M., Late Pleistocene technology, economic behavior and land-use dynamics in southern Italy, *Am. Antiquity* **69** (2004) 273–290.

[95] Riel-Salvatore, J. and Barton, C. M., New quantitative perspectives on the Middle-Upper Paleolithic transition: The view from the northern Mediterranean, in *Early Upper Paleolithic "Transitional" Industries: New Questions, New Methods*, Riel-Salvatore, J. and Clark, G. A. (eds.) (British Archaeological Reports, Oxford, 2007).

[96] Riel-Salvatore, J. and Clark, G. A., *New Approaches to the Study of Early Upper Paleolithic "Transitional" Industries in Western Eurasia. Transitions Great and Small* (Archaeopress, Oxford, 2007).

[97] Riel-Salvatore, J., Popescu, G. and Barton, C. M., Standing at the gates of Europe: human behavior and biogeography in the Southern Carpathians during the Late Pleistocene, *J. Anthropol. Archaeol.* **27** (2008) 399–417.

[98] Sandgathe, D. M., *Examining the Levallois Reduction Strategy from a Design Theory Point of View* (Archaeopress, Oxford, 2006).

[99] Shott, M. J., An exegesis of the curation concept, *J. Anthropol. Res.* **52** (1996) 259–280.

[100] Shott, M. J., Lower Paleolithic industries, time and the meaning of assemblage variation, in *Time in Archaeology: Time Perspectivism*, Holdaway, S. and Wandsnider, L. (eds.) (University of Utah Press, Salt Lake City, 2008), pp. 61–75.

[101] Shott, M. J. and Sillitoe, P., Use life and curation in New Guinea experimental used flakes, *J. Archaeol. Sci.* **32** (2005) 653–663.

[102] Shott, M. J. and Weedman, K. J., Measuring reduction in stone tools: an ethnoarchaeological study of Gamo hidescrapers from Ethiopia, *J. Archaeol. Sci.* **34** (2007) 1016–1035.

[103] Speth, J. D., Experimental investigations of hard-hammer percussion flaking, *Tebiwa* **17** (1974) 7–36.

[104] Stewart, J. R., The ecology and adaptation of Neanderthals during the non-analogue environment of Oxygen Isotope Stage 3, *Quatern. Int.* **137** (2005) 35–46.

[105] Stiner, M. C. and Kuhn, S. L., Changes in the "connectedness" and resilience of Paleolithic societies in Mediterranean ecosystems, *Hum. Ecol.* **34** (2006) 693–712.

[106] Straus, L. G., A mosaic of change: The Middle-Upper Paleolithic transition as viewed from New Mexico and Iberia, *Quatern. Int.* **137** (2005) 47–67.

[107] Tattersall, I., Neanderthal skeletal structure and the place of Homo neanderthalensis in European hominid phylogeny, *Hum. Evol.* **21** (2006) 269–274.

[108] Tomasello, M., The human adaptation for culture, *Annu. Rev. Anthropol.* **28** (1999) 509–529.

[109] Trinkaus, E., Early modern humans, *Annu. Rev. Anthropol.* **34** (2005) 207–230.

[110] Vanharen, M., The evolutionary significance of beadmaking and use, in *From Tools to Symbols: From Early Hominids to Modern Humans*, d' Errico, F. and Blackwell, L. (eds.) (Witwatersrand University Press, Johannesburg, 2005), pp. 525–535.

[111] Villa, P., Lenoir, M., Hublin, J.-J. and Richards, M. P., Hunting and hunting weapons of the lower and Middle Paleolithic of Europe, in *The Evolution of Hominin Diets: Integrating Approaches to the Study of Palaeolithic Subsistence* (Springer, New York, NY, 2009), pp. 59–85.

[112] Villaverde, V., Aura Tortosa, J. E. and Barton, C. M., The Upper Paleolithic in Mediterranean Spain: A review of current evidence, *J. World Prehist.* **12** (1998) 121–198.

[113] Voisin, J.-L., Speciation by distance and temporal overlap: a new way of understanding Neanderthal evolution, in *Neanderthals Revisited: New Approaches and Perspectives*, Harisson, T. and Harvati, K. (eds.) (Springer, New York, 2006), pp. 299–314.

[114] Wall, J. D., Lohmueller, K. E. and Plagnol, V., Detecting ancient admixture and estimating demographic parameters in multiple human populations, *Mol. Biol. Evol.* **26** (2009) 1823–1827.

[115] White, J. P. and Thomas, D. H., What mean these stones? Ethno-taxonomic models and archaeological interpretations in the New Guinea Highlands, in *Models in Archaeology*, Clarke, D. L. (ed.) (Methuen, London, 1972).

[116] Whittaker, J. C., *Flintknapping: Making and Understanding Stone Tools* (University of Texas Press, Austin, 1994).

[117] Wilensky, U., *NetLogo* (Center for Connected Learning and Computer-Based Modeling, Northwestern University, 1999).

[118] Wolf, D. E., Takebayashi, N. and Rieseberg, L. H., Predicting the risk of extinction through hybridization, *Conserv. Biol.* **15** (2001) 1039–1053.