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Dispersal and the Movius Line: testing the effect of dispersal on population density through simulation

Iza Romanowska[1, 2] *, Clive Gamble[2], Seth Bullock[3], Fraser Sturt[2]

[1]*Institute for Complex Systems Simulation, University of Southampton, UK*
[2]*Department of Archaeology, University of Southampton, UK*
[3]*Department of Computer Science, University of Bristol, UK*

Abstract

It has been proposed that a strong relationship exists between the population size and density of Pleistocene hominins and their competence in making stone tools. Here we focus on the first 'Out of Africa' dispersal, 1.8 Ma ago, and the idea that it might have featured lower population density and the fragmentation of hominin groups in areas furthest away from the point of origin. As a result, these distant populations in Central and East Asia and Europe would not be able to sustain sophisticated technological knowledge and reverted to a pattern of simpler stone-knapping techniques. This process could have led to the establishment of the 'Movius Line' and other long-lasting continental-scale patterns in the spatial distribution of Lower Palaeolithic stone technology.

Here we report on a simulation developed to evaluate if, and under what conditions, the early 'Out of Africa' dispersal could lead to such a demographic pattern. The model comprises a dynamic environmental reconstruction of Old World vegetation in the timeframe 2.5-0.25 Ma coupled with a standard biological model of population growth and dispersal. The spatial distribution of population density is recorded over the course of the simulation. We demonstrate that, under a wide sweep of both environmental and behavioural parameter values, and across a range of scenarios that vary the role of disease and the availability of alternative crossing points between Africa, Europe and Asia, the demographic consequence of dispersal is not a gradual attenuation of the population size away from the point of origin but a pattern of ecologically driven local variation in population density. The methodology presented opens a new route to understand the phenomenon of the Movius Line and other large-scale spatio-temporal patterns in the archaeological record and provides a new insight into the debate on the relationship between demographics and cultural complexity. This study also highlights the potential of simulation studies for testing complex conceptual models and the importance of building reference frameworks based on known proxies in order to achieve more rigorous model development in Palaeolithic archaeology and beyond.

*Corresponding author: i.romanowska@soton.ac.uk

1. Introduction

Recently, there has been a sharp increase in the number of archaeological models using population dynamics to explain patterns in archaeological data such as complexity of toolkits, technological stasis and 'innovation revolutions' or stylistic variability within and between assemblages (Neiman 1995; Shennan 2000; 2001; Henrich 2004; Kline and Boyd 2010; Andersson 2011; Premo 2012; Vaessen 2012; Andersson and Read 2014; Querbes et al. 2014; Peña and Nöldeke 2016).

Formal mathematical models show that population size can impact on a group's cultural repertoire due to random drift (Neiman 1995; Shennan 2000; 2001) and variability in cultural transmission (Henrich 2004). These models propose that larger groups tend to have a higher number of individuals with any given trait, and hence they are less likely than smaller groups to lose their genetic and cultural diversity due to random sampling (Shennan 2001). Second, passing sophisticated technology from one generation to the next follows a distribution in which most of the learners perform worse than the teacher but the general tendency for informational/cultural deterioration can be counteracted by occasional events, such as perfect replication or innovation associated with exceptional individuals. The larger the group, the higher the rate of such events or individuals, hence maintaining sophisticated technology is easier to achieve (Henrich 2004). Conversely, if the population size (defined as the number of individuals involved in cultural transmission) and population density, occasionally termed together as 'social interconnectedness', are not high enough this may lead to a loss of knowledge and skill in the group. A number of additional factors and processes may influence the rate of cultural transmission and innovation, such as the cultural hitchhiking of neutral traits, the cost of retaining cultural complexity in the long term or the mechanisms eliminating errors in transmission, and their relative importance has been modelled and discussed by a number of authors (e.g., Andersson 2011; Mesoudi 2011; Premo 2012)

Although the models are, for the most part, rigorously developed using formal methods, their validity within the archaeological context depends on correct estimates of population size, density and interconnectedness. In some cases, when a written record is available one can make reliable estimates easily (Henrich 2004). For more distant time periods demographic proxies (Davies et al. 2015; Shennan 2001) or genetic estimates have been used (Powell et al. 2009). Going even deeper into the past, prior to the Upper Pleistocene these proxies are unavailable, and population size must be estimated on the basis of more general processes and factors impacting population dynamics on the large scale (Davies et al. 2015).

Such estimates may be derived from general ecological principles of population dynamics, such as the total carrying capacity of a given environment. Equally, other physical, social and environmental processes are likely to exert significant influence on population dynamics at the scales relevant to the study of Pleistocene hominins. One such large-scale process, which has been proposed as a potential driver of demographic trends at a species-level, is dispersal (e.g., Lycett and Cramon-Taubadel 2008; Smith et al. 2009; Lahr 2010; Lycett and Bae 2010; Lycett and Norton 2010; Groucutt and Petraglia 2012; Huguet et al. 2013).

The aim of this study is to evaluate if and under what conditions dispersal had a significant impact on population densities of Pleistocene hominins using the case study of the first 'out of Africa' dispersal. The null model investigated here proposes that dispersal leads to a decrease in the population size and density proportionally to the distance from the point of origin. That is, we expect to see a gradient-like thinning of the population along the dispersal path. In addition, two alternative scenarios were tested with different exit points out of Africa (Gibraltar, Mandeb and Hormuz Straits) and the possibility of disease alleviation beyond the tropical belt.

A number of conceptual models linking dispersal to a drop in population size and density have been proposed before (Bar-Yosef et al. 2012; Lycett and Bae 2010; Lycett and Norton 2010), but, to the best of our knowledge, the relationship between these two phenomena has never been formally tested in the context of Pleistocene hominin groups (cf. Hazelwood and Steele 2004; Smith et al. 2009). Equally, previous models of early Pleistocene dispersals (e.g., Mithen and Reed 2002; Smith et al.
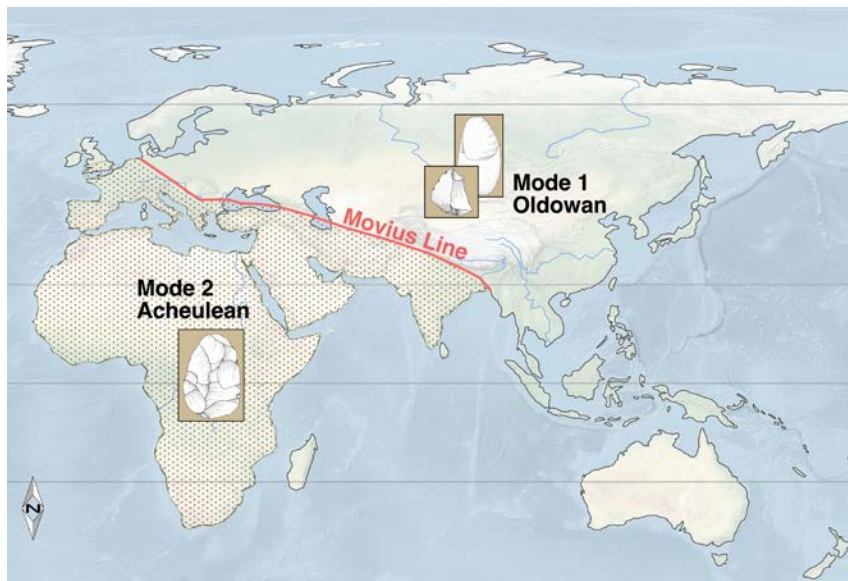
Figure 1. *The extent of the Movius Line in the Lower and Middle Pleistocene. The background map: naturalearthdata.com.*

2009; Wren et al. 2014) focused on aspects of the dispersal process other than population dynamics.

The null model provides a data prediction specific to the case study. If in areas further away from the East African origins of the first hominin dispersal two million years ago the hominin population was fragmented into smaller (lower population size) and more dispersed (lower population density) groups, it is conceivable that the associated weakening of the cultural transmission processes could have led to significant losses in cultural repertoire and to the inability of groups to maintain more sophisticated technology. The result of such a mechanism would be visible in the archaeological record as a regression from the more sophisticated tool making behaviour requiring a high level of cultural transmission observed near the dispersal origin to a simpler knapping strategy observed further from the original home-range of hominins.

An example of such a pattern is the observed spatial distribution of Mode 1 and Mode 2 assemblages during the Lower Pleistocene known as the 'Movius Line' (Figure 1) (Movius, 1944; 1948; Schick, 1994; Keates, 2002; Dennell, 2009; Brumm, 2010; Lycett and Bae, 2010). Although, there is increasingly strong evidence (Brumm and Moore, 2012; Zhang et al. 2010; Li et al. 2012; Wei et al. 2015) for rare occurrences of Mode 2 toolkits on the

'wrong' side of the Movius Line (and vice versa), the general pattern of Mode 2 assemblages being disproportionally more frequent south and west of the Movius Line remains strong.

The value of using population dynamics to interpret patterns in the Palaeolithic record has been questioned (cf. Collard and Wood 2000; Collard et al. 2005; 2013a; 2013b; Derex et al. 2013; Muthukrishna et al. 2013; Andersson and Read 2014). However, what emerges is an urgent need for a better understanding of what potential mechanisms influence population size and density on a large spatio-temporal scale in order to establish if the postulated demographic pattern existed in the first place (Bar-Yosef et al. 2012). The goal of this paper is to examine the causal relationship between dispersal - an archaeologically attested large-scale process that affected early hominins - and the population dynamics of the dispersing hominin groups. The results, in turn, could be used to inform future models that use population dynamics to model different aspects of hominin lives, and allow them to relate to the archaeological record in a more meaningful way or with a higher degree of certainty.

2. Modelling Large Scale Ancient Human Dispersals

The demographic disparity between regions separated by the Movius Line is proposed on the

basis of an assumption that East Africa was the starting point of the dispersal and a hypothesis that dispersal caused a gradual thinning of the population away from the East African point of origin towards Europe and East Asia.

The aim of our study is to provide a quantitative assessment of this null model by means of computational modelling. We simulate the first 'Out of Africa' dispersal, compare population densities in the Mode 1 and Mode 2 regions throughout the simulated period of time, and evaluate whether or not the proposed demographic disparity marked by the Movius Line is plausible and, if so, what possible mechanisms could be driving it.

Computational modelling (simulation) is an increasingly important approach in archaeology to the challenges of researching complex systems, that is systems in which numerous individual parts interact with each other in a non-linear way, producing aggregated behaviour that cannot be easily predicted solely on the basis of their individual characteristics (Mitchell, 2009, pp.12-4; Barton, 2014). A number of simulation techniques have been used before to investigate various aspects of human mobility patterns and different ancient dispersals (overview in: Romanowska 2015a), including equation-based modelling (e.g., Steele et al. 1998; Steele 2009; Fort 2012), cellular automata (e.g., Mithen and Reed 2002; Nikitas and Nikita 2005) and agent-based modelling (e.g., Wren et al. 2014; Scherjon 2013) or a combination of the above (e.g., Young 2002; Callegari et al. 2013). Similarly, this model shares a number of features with all of the three most commonly used approaches - cellular automata, equation-based modelling and individual-based modelling.

Computational modelling enables dynamical systems to be represented and explored in a formal way that addresses some of the complexity of the studied phenomena. It can overcome many of the limitations of traditional conceptual, descriptive methods and bypass some of the intrinsic biases of the archaeological data. For example, simulation can be used as a theory building tool, in a form of a 'virtual lab' to test conceptual models and to recognise their implications, in particular those that would have left traces in the empirical record (Di Paolo et al., 2000; Epstein, 2006; Premo, 2006).

Equally, this method helps to tackle the complexity of the system by testing the consequences of the, often non-linear, interplay between the system entities and the postulated rules guiding their relationships, therefore, enabling researchers to move beyond simple intuitive models. Finally, even the formalisation of a hypothesis, which is necessary before it can be coded into a simulation, helps to identify in a formal way key entities and relationships in the system, and opens the door for better structured discussion and the application of other quantitative methods. A computer model can be constructed to test any proposed mechanism, e.g., dispersal causing gradual attenuation of the population away from the point of origin.

One of the common procedures in computational modelling is to build a simple abstract model developed 'from first principles' in order to construct a theoretical framework combining proxy data with information coming from, e.g., the archaeological record. The aim of this method is to test if the assumptions we hold about how the system works are correct and to identify irregularities in the data. The simulation produces a 'benchmark' of what we expect the empirical data to look like given our theoretical assumptions regarding the system. If those two do not match, it indicates that either our understanding of the system is incorrect or the data we compared the simulation to are not representative of the real phenomenon in question. This benchmark can be further used to evaluate (but not empirically test) archaeological hypotheses. Here we applied the standard biological models of population growth and dispersal that are used to represent population dynamics of all animal species including humans (Snider and Brimlow 2013).

Although in theory all combinations of parameter values could be tested, in practice models are often parameterised using ranges of values derived from empirical data. If these are unavailable, proxy data are commonly used. Data coming, for example, from research on modern hunter-gatherers, although often described as too complex to be meaningfully translated into archaeological studies (e.g., Kelly, 2013), are often used to structure archaeological discourse about the Palaeolithic. Humans in the present are still a better approximation for humans in the past (and their ancestors) than any other living species. Therefore

we used aggregate data from a large sample of modern hunter-gatherers (Binford, 2001) to give us an idea of the range of human variability as well as its lower and upper boundaries. These values were then transformed into model parameters.

Although computational modelling has its own limitations and misapplications, it is currently one of the best methods available for investigating the way in which low-level interactions give rise to population-level, global patterns in complex systems, of which past human societies are undoubtedly an example. As such, it has an enormous potential for disciplines such as archaeology, which strive to uncover and understand such mechanisms but must rely on non-systematic and incomplete data. This study illustrates how simulation techniques drawn from complexity science can help to move archaeological research beyond intuitive, descriptive models.

3. Description of the Model

The simulation involves two main model entities: i) a spatially distributed population of hominin groups that grow through reproduction and disperse across a grid representing the globe, and ii) a sequence of friction maps representing the changing environment within which the hominins are distributed. The model is initialised with hominins concentrated in a small area in East Africa and an initial friction map representing the environmental biomes of each cell in the grid. The model then runs for 2250 steps representing the time span between 2.5 and 0.25 Mya. At each step, and for each cell in the grid, the hominin population is updated as a result of growth and dispersal, both of which are influenced by the environmental character of the cell. Every 10 steps, the friction map is updated to reflect environmental change. At each time step, a proportion of each cell's population (dependent on that cell's biome) will spread from its initial location in random directions. As a result, hominins will more readily spread through areas that are more favourable to them. The detail of the particular spatio-temporal pattern of dispersal that arises is determined by model parameters governing the growth rates, dispersal rates, and carrying capacities associated with different biomes. A basic description of the model is given below. For full details see the Supplementary Material A: Methods.

3.1. The environment

The null model proposes that hominin population dynamics are primarily driven by biogeographic factors: ecological conditions and topographic barriers (Binford, 2001, p.151; Mithen and Reed, 2002; Holmes, 2007). Therefore, a sequence of global friction maps representing the dynamically changing environment throughout one glacial-interglacial cycle (Bridge 2014) was mapped onto the temperature curve of the Lower and Middle Pleistocene (Bintanja and van de Val, 2008). The maps incorporate: i) changes in the shape of continents, driven by sea level fluctuations, and ii) changes in the extent and distribution of different ecological conditions, represented by eight different *biomes* that provide the ecological context for hominin growth and dispersal (tropical, warm temperate, equatorial, sub-tropical, desert, cold temperate, boreal, polar; plus a ninth category representing inaccessible bodies of water or ice). Since there is a high level of uncertainty associated with environmental reconstructions derived from GCMs (Global Circulation Models), we conducted a series of tests which determined that this environmental reconstruction of the Pleistocene glacial cycles did not have significant impact on the general results reported here (see Supplementary Information A: Methods for more details).

3.2. Growth and dispersal

The size of the hominin population at grid cell i is represented by $P_i \geq 0$. At each time step, for each cell i with biome b, the population P_i is updated by two processes: i) growth and ii) dispersal. Growth is determined by a biome-specific growth rate r_b, and is proportional to population size. It is capped by the carrying capacity of the cell, K_b, which is also specific to the cell's current biome. Dispersal is achieved via simple diffusion, with a biome-specific proportion, D_b, of the population in each cell being allocated equally between the subset of neighbouring cells (i.e., cells in the von Neumann neighbourhood: North, South, East, or West) that are available for dispersal, (i.e., cells that are not Water/Ice).

3.3. Parameterisation

The parameter values used in this study derive from an aggregation of data on over 250
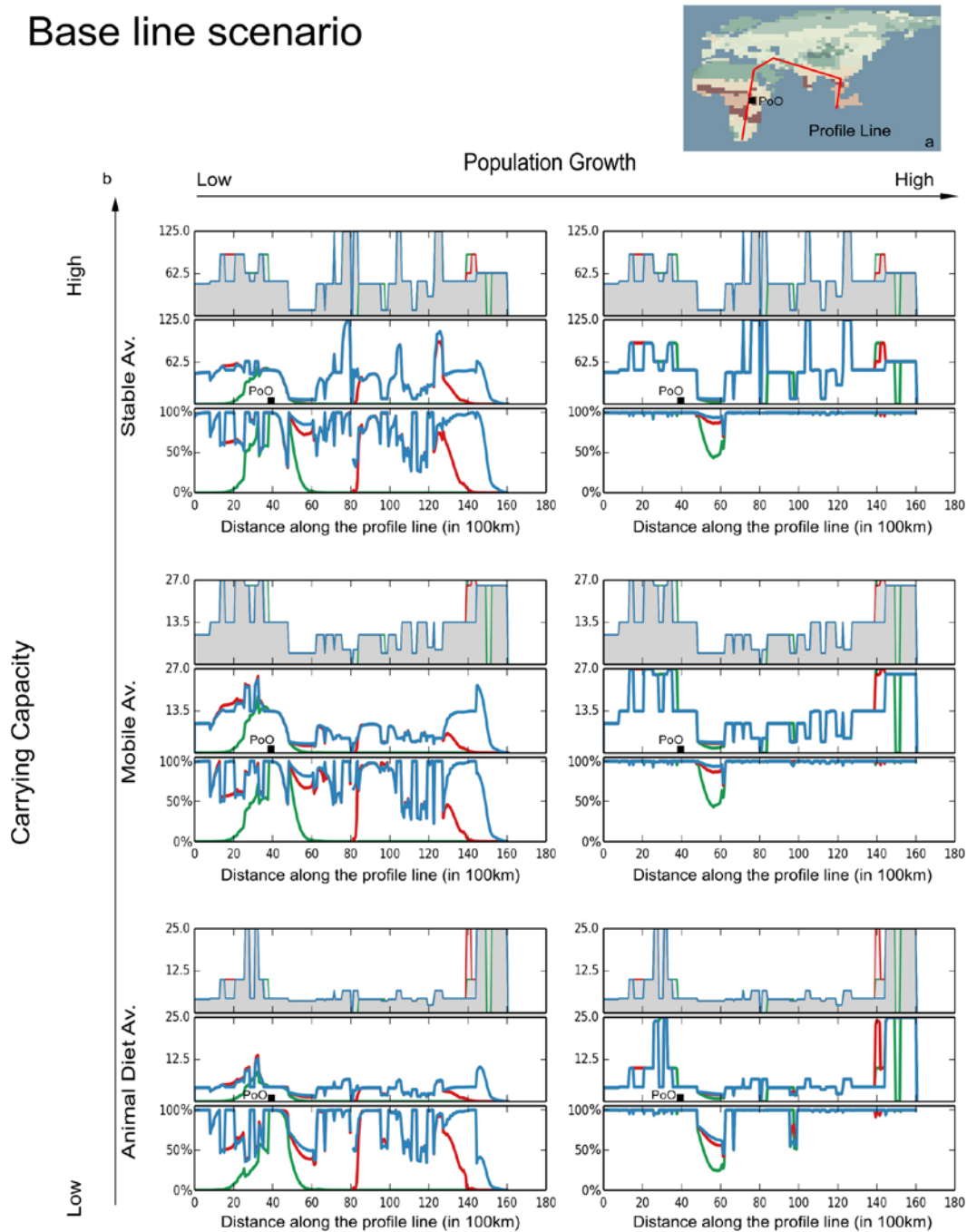
Figure 2. *a) The 18,000km long profile line; the starting point 0 is located in South Africa, the end point is in South-East Asia. PoO – Point of Origin of the dispersal, 4,000km along the profile line. b) Graph showing six of the tested scenarios: high or low population growth combined with minimum (Animal Diet Av.), maximum (Stable Av.) or intermediate (Mobile Av.) carrying capacity (for a detailed breakdown of the values see Supplementary Information A: Methods. Section: "Carrying capacity"). For each scenario, we plot carrying capacity (top), simulated population size (middle) and population size as a percentage of carrying capacity (bottom) along the profile line (shown in red on the inset map - a). Each plot shows three profiles: 2 Mya (green), 1 Mya (red) and 0.5 Mya (blue);*
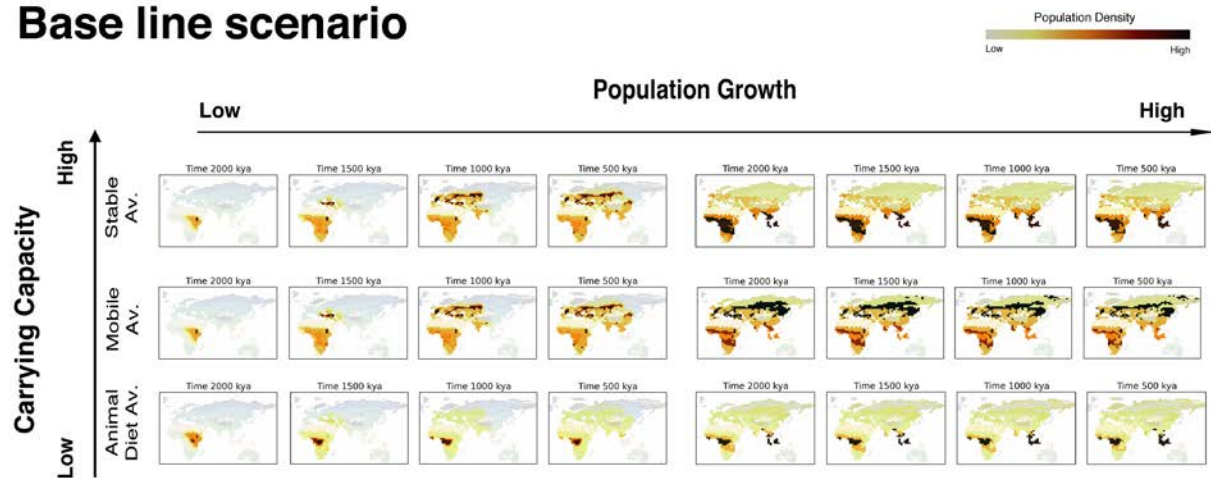
Figure 3. *Chronological map series for each of the six simulated scenarios depicted in Figure 2. Each map shows the distribution of the hominin population, with colours indicating the underlying biome and colour intensity reflecting population size.*

modern hunter-gatherer groups collated by Binford (2001). These values are integrated into the friction map, which combines a number of demographic parameters: the suitability of each biome for hominin occupation (*carrying capacity* and *population growth* rates) and the level of hominin adaptation to a given environment (*diffusion rate*). Further details of model parameters are given in the Supplementary Information A: Methods.
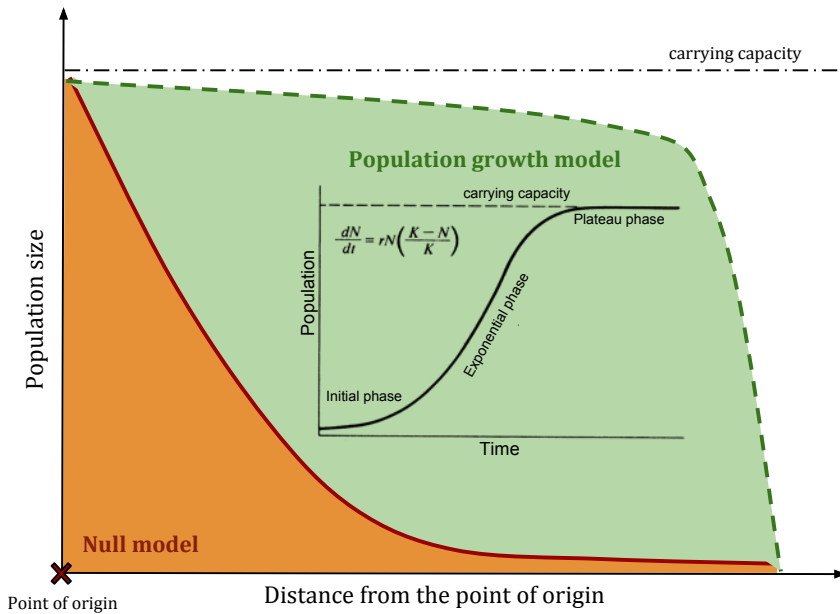
4. Results

The raw output of the model is an array representing the hominin population size at each grid cell at each time step. In order to more easily compare results across multiple scenarios, a profile of population density (Figure 2b) along an 18,000 km long line crossing through Africa and Asia was created (Figure 2a).

Distance from the point of origin in East Africa is not a reliable predictor of population density in any of the tested scenarios (see Figures 2 and 3). Instead, the most striking feature of the population dynamics in all scenarios is how quickly the hominin population reaches the carrying capacity of occupied cells. This can be evaluated by noting the similarity between the upper plot for any of the six scenarios depicted in Figure 2 (showing the profile of the carrying capacity along the profile line) and the

associated middle plot depicting the population size at three points in time. The relationship between these two properties is summarised in the bottom plot for each scenario, showing what percentage of the overall carrying capacity is accounted for by the hominin population at the same three points in time. In general, this occupancy value is high, ranging from 50%-100% across low-growth scenarios and is close to 100% for high growth scenarios.

This is not a surprising result if one compares it to the standard population growth curve (Figure 4). Once the population size exceeds the slow initial phase, the growth follows an exponential curve (i.e., a phase of fast increase) before it reaches the plateau phase as it approaches the carrying capacity ceiling. Given the relationship between the growth and dispersal rates, and the spatial and temporal scales, in all tested scenarios the hominin population size tends to be at or around the carrying capacity ceiling of the environments that they occupy. In addition, we can see that the population growth rate has the strongest impact on the propagation speed of the dispersal wave, since in all of the higher population growth rate (based on observed hunter-gatherer population growth) scenarios the Old World is almost entirely populated by 2 Mya (Figures 2 and 3, high population growth scenarios represented in the right-hand side column).

Population size / Distance from the point of origin

Null model

Point of origin

carrying capacity

Population growth model

carrying capacity

$\frac{dN}{dt} = rN\left(\frac{K-N}{K}\right)$

Plateau phase

Population

Exponential phase

Initial phase

Time

Figure 4. *Schematic representation of the null model (the orange graph) in which there is a gradient in population size stretching from the point of origin of the first dispersal compared to the prediction of the standard population dynamics model (shown graphically inside the figure) as implemented in this simulation in green.*

The fluctuations in the results, particularly noticeable in scenarios where the carrying capacity is close to the bottom of the tested range, are due to the dynamic nature of the underlying friction map changing the local conditions occasionally, thus forcing the population numbers to very small values. Interestingly, the biggest differences can be observed in areas with a particularly low carrying capacity – reflecting the time required to rebuild a population from very small numbers (i.e., during the initial phase on the population growth curve). This is a good example of the complexity and non-linearity in the relationships between different factors and the population size. Nonetheless, the pattern of population density tracking the carrying capacity ceiling is robust enough that it arises in even the most extreme scenarios.

In fact, in order to force a population distribution that exhibits a gradient such that distance from the African dispersal origin is a good predictor of population density, we must explore population growth rates that are significantly far (orders of magnitude removed) from reasonable estimates. For example, when population growth rates are reduced proportionately such that they are one hundred times lower than in the low growth scenario the population fails to leave Africa and the population profile only exhibits the required

gradient within a small area at the front of the dispersal wave.

5.   Testing alternatives

In the conceptual model defined above, in order for the distance from the point of origin to play a key role in shaping population density, the wave of dispersal needs to have the shape of a very long, gradually declining front where population size is kept well below its carrying capacity and a gradient of decreasing population density extends from Africa towards the Asian and European outskirts (Figure 4). In the current simulation even a small initial population consistently reached their carrying capacity in a relatively short time span. If, therefore, a population gradient from Africa to the Asian and European outskirts does not arise as a consequence of basic growth and dispersal: what other factors could produce a similar pattern? Although many scenarios can be proposed, here we explore two candidates: the *straits scenario* and the *disease scenario*. For the following simulation runs a simplified population growth algorithm was used (see the Methods section). However, the results remained qualitatively similar. The remainder of the simulation setup is the same as described in section 3 apart from the alterations described below.
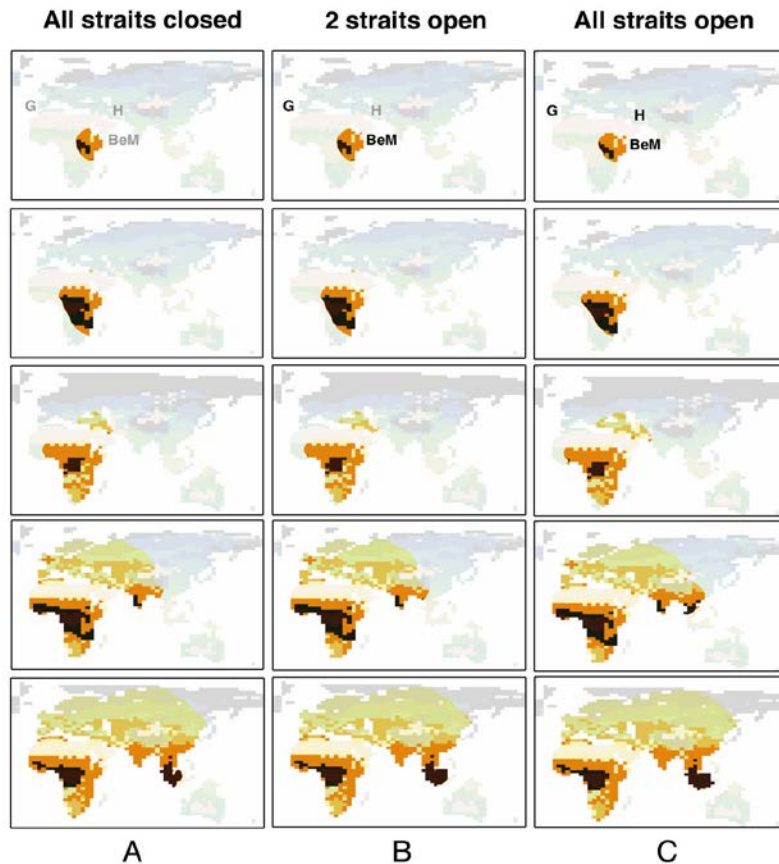
Figure 5. *Three versions of the straits scenario (depicted run: high population growth, high carrying capacity): a) All straits closed for hominin dispersal; b) The Strait of Gibraltar and the Strait of Bab el-Mandeb open; c) All straits open for hominin dispersal. G – the Strait of Giblartar; H – the Strait of Hormuz; BeM – the Strait of Bab-el-Mandeb.*

5.1 The straits scenario

The impact of ocean straits on hominin dispersal has been extensively discussed in the past (e.g., Villa, 2001; Derricourt, 2005). The straits scenario follows these descriptive models in investigating the effect that sea crossings could have on the overall pattern of dispersal, the 'bottleneck' regions and the general population dynamics on both sides of the Movius Line. Three scenarios were tested. Firstly, all straits (the Gibraltar, the Bab-el-Mandeb and the Hormuz) were closed for hominin movement. Secondly, the two most often invoked sea crossings, the Gibraltar and the Bab-el-Mandeb straits, were opened for dispersal. Finally, the third scenario included an additional opening of the Strait of Hormuz. In each of these new scenarios, the straits were permanently bridged by cells exhibiting the biome of the adjacent existing land either side of the straits. Each of these land bridges amounted to altering a small number of Water cells such that they permanently exhibited a traversable biome.

None of the three tested scenarios managed to replicate a spatial pattern exhibiting a gradual decrease of population size away from Africa (Figure 5). However, they revealed some unanticipated spatial and temporal patterns of the dispersal. Surprisingly, the opening of the straits to hominin movement produced no significant differences in the results compared to the baseline scenario (all straits closed to hominin movement, Figure 5a) including the timing of the arrival of the dispersal wave in Europe and South-East Asia (Figure 5b). The timing of peopling of the westernmost part of Europe and the easternmost edge of South-East Asia differed between the scenarios by less than 50ka.

It is likely that the pattern of dispersal into Europe arriving from the east rather than from the south is caused by the impact of the Sahara Desert. The Sahara, being a significant barrier due to the low population growth rate associated with
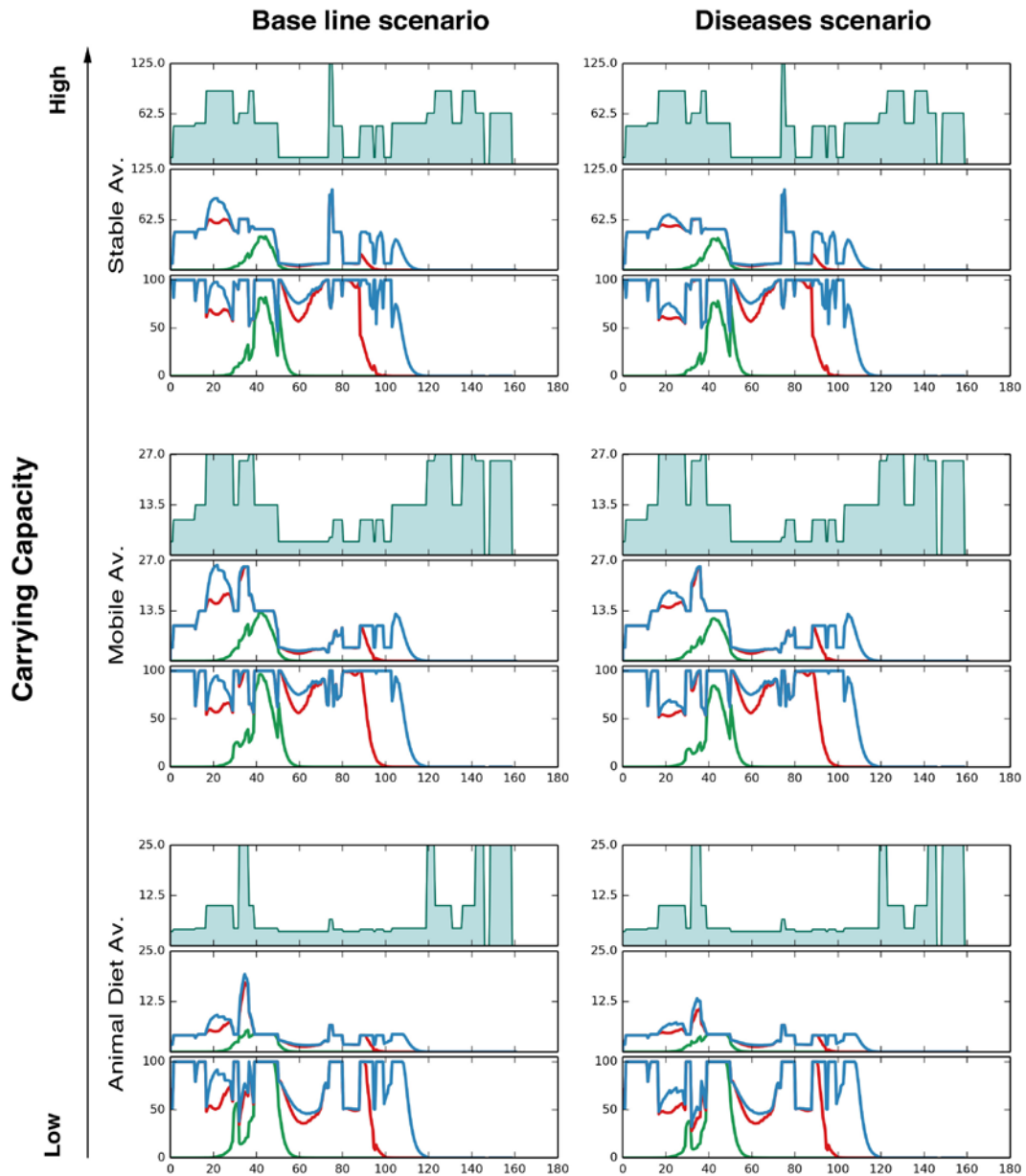
Figure 6. *The disease scenario (right hand column) compared with the baseline scenario, runs with low population growth (left hand column). See figure 2 for details.*

the Desert biome, slows dispersal to such an extent that hominins dispersing via the Levant and the Anatolian Peninsula, and thereby arriving in Europe from the south-east, are able to reach the continent at roughly the same time as those dispersing via the Strait of Gibraltar. This in itself shows that, contrary to the null model's prediction, Central and Eastern Europe (dominated by Mode 1-type artefacts and therefore being on the hypothesised less densely populated side of the Movius Line) is not further away from the point of origin of the dispersal than Western Europe whether or not the Strait of Gibraltar remains open for hominin movement (cf. Romanowska 2015b).

In the east, the Arabian route is often considered a 'fast-track' to Asia (Petraglia, 2003; Field and Lahr, 2005). However, the simulation shows that first, this depends on the opening of both the Strait of Bab-el-Mandeb and the Strait of Hormuz, and second, it makes little difference overall. If only the Bab-el-Mandeb Strait is open to hominin movement (Figure 5b), by the time the dispersal front reaches the northern edge of the Arabian Peninsula, the wave arriving via modern Egypt is already there. Thus the front of the dispersal appears in the same place as in the baseline "no straits" scenario (Figure 5a). Without the opening of the Strait of Hormuz, rarely mentioned in the literature, the Arabian route does not speed up the dispersal into Asia at all. However, even if both straits are open, the difference in the timing of arrival of the dispersal wave in modern day India and further on is hardly significant (Figure 5c).

5.2 The disease scenario

The disease scenario investigates the impact of one of the prime factors curbing population numbers: pathogens and parasites. It has been argued (Bar-Yosef and Belfer-Cohen, 2000) that leaving the tropical 'disease belt' might have ignited a population boom in the cooler and drier temperate zone where population growth is less affected by zoonotic diseases (i.e., those transmitted from non-human animals to humans) and parasites. This factor is to some extent already incorporated in the model as differences between the population growth rates in different biomes. These values, derived from both modern hunter-gatherers and Palaeolithic estimates, reflect population dynamics influenced by many factors including the impact of pathogens (Binford, 2001). Nevertheless, due to its potentially high impact we decided to test if intensifying the repercussions of increased susceptibility to pathogens could alter the global patterns of population dynamics.

The simplest implementation was used. Population growth was halved in the 'disease belt', i.e., equatorial and tropical zones where the pathogens and parasites are particularly rampant (Bar-Yosef and Belfer-Cohen, 2000). Despite this substantial alteration, the results are virtually indistinguishable from the baseline scenario (Figure 6). Again, the strength of the exponential rate of population growth dominates any other effect, highlighting the robustness of the underlying mechanism of population size quickly approaching the carrying capacity ceiling.

6. Discussion and conclusions

In this study we have re-evaluated a null model proposing that the main demographic factor impacting the hominin population density during the Pleistocene is the distance from the point of origin of the first 'Out of Africa' dispersal. Under the broad conditions imposed by the model presented here, this notion seems unlikely. The simulation scenarios fail to exhibit the necessary gradient from the more densely populated African centre towards less populated European and Asian outskirts. Moreover, the general population dynamics of the model indicates that to achieve such a gradient through dispersal and growth alone is not possible within a realistic range of parameter values. Instead the simulation suggests that, even with very low population growth, carrying capacity can be achieved very quickly after the initial colonisation of a new area. This results in a steep dispersal front. As such, this study identifies the carrying capacity of the hominin environment and hominin population growth as two dominant factors in the population dynamics of early hominin groups. This is consistent with earlier work on population dynamics and dispersals (Snider and Brimlow 2013; Hazelwood and Steele 2004). It is important to stress that these findings do not directly address the findings of cultural transmission models discussed in the introduction, as the relationship between population size and the complexity of lithic assemblages has not been the topic of this study. While the model presented here suggests that census population may not be negatively correlated with distance from the dispersal origin, it may remain the case that the capacity of groups to maintain sophisticated tool use is negatively correlated with this distance due to a fall in population size in unfamiliar environments, or fragmentation of groups, or eroded social organisation, or some other demographic factor. Equally, the model presented here does not disprove the proposition that the Movius Line was caused by differences in population density, and, until more empirical data enables us to reconstruct the Pleistocene environments on each side of the Movius Line, it remains agnostic as to whether or not

regions differed in terms of their population density. Instead, what we show here is that <u>if there was</u> a variability in hominin population density during the Lower and early Middle Pleistocene, it was likely to be related to factors <u>other than</u> the distance from East Africa and the first 'out of Africa' dispersal, for example the local environmental conditions and the hominin level of adaptation. Although the evaluation of two alternative factors performed in this study did not yield satisfactory explanations, other, more complex scenarios, involving such factors as the impact of particular topographic and ecological features, competition with members of the carnivore guild, specific cultural adaptations or dependence on social networks (e.g., Turner, 1999; Arribas and Palmqvist, 1999; de Lumley, 2006, Smith et al. 2009), falling outside the scope of this simulation study, should be considered.

In light of this model's results, the next step would be to focus on the differences in relative carrying capacity between the regions either side of the Movius Line. These carrying capacities are dependent on the biomass of the environment and the organism's ability to extract energy from it. Thus, a combination of these two factors (e.g., lower biomass of the temperate zone combined with the lack of hominin adaptation strategies for the south-east Asian tropical forest) could cause significantly lower values of the hominin carrying capacity in the environments on the Mode 1 side of the Movius Line compared to the values used in this simulation (which were based on well-adapted modern hunter-gatherers). In this scenario, the occasional appearance of Mode 2 implements on the 'wrong' side of the Movius Line could be associated with environmental pockets of more favourable conditions. In fact, both Korean and Indonesian assemblages with handaxes were found on sites associated with open landscapes (Norton et al., 2006), and Brumm (2010) shows that the current extent of the South East Asian tropical rainforest does not reflect the more open and mosaic conditions of the Early and Middle Pleistocene. As the environmental reconstruction used in this simulation lacks such Pleistocene-specific features (another example would be the South Asian 'savannah belt', Dennell and Roebroeks, 2005; Lahr, 2010), this hypothesis cannot be evaluated within the current implementation.

The results of this study suggest that in order to fully test the hypothesis linking the Movius Line with varying levels of population density of the hominin groups, in addition to more archaeological survey on the eastern Mode 1 side of the Movius Line our focus should also be on more precise environmental reconstruction. If paired with the population dynamics framework developed here, it could shed light on the complex relationship between the environment, the demography and the cultural evolution of early hominins (for similar conclusions, see Smith et al. 2009). Equally, identifying archaeologically visible processes that cause demographic perturbations may provide more evidence in the on-going debate on the relationship between technological complexity and population size.

This study stresses the complex nature of past interactions and highlights the capacity of simulation techniques as the flexible scientific method that can tackle various causal mechanisms and combine multiple strands of evidence within a formal framework. Computational modelling has the potential to propel the debates about the Movius Line and other large scale spatio-temporal patterns away from simplistic 'one factor explains all' hypotheses towards multiple-factor models, and quantitatively tested scenarios, much more likely to reflect the complexity of hominin lives during the Pleistocene.

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