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

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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.

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

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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 (Shennan, 2001; Davies et al., 2015) 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 (Lycett and Bae, 2010; Lycett and Norton, 2010; Bar-Yosef et al., 2012), 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., 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' (Fig. 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., 2014; 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., Scherjon, 2013; Wren et al., 2014) 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.