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The role of spatial foresight in models of hominin dispersal

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ABSTRACT

Increasingly sophisticated hominin cognition is assumed to play an important role in major dispersal events but it is unclear what that role is. We present an agent-based model showing that there is a close relationship between level of foresight, environmental heterogeneity, and population dispersibility. We explore the dynamics between these three factors and discuss how they may affect the capacity of a hominin population to disperse. Generally, we find that high levels of environmental heterogeneity select for increased foresight and that high levels of foresight tend to reduce dispersibility. This suggests that cognitively complex hominins in heterogeneous environments have low dispersibility relative to cognitively less complex organisms in more homogeneous environments. The model predicts that the environments leading up to major episodes of dispersal, such as the initial hominin dispersal into Eurasia, were likely relatively low in spatial heterogeneity and that the dispersing hominins had relatively low foresight.

Introduction

The relationship between increasing cognitive complexity of hominins and their ability to adapt to complex and heterogeneous environments has been a focus of palaeoanthropological research in general (Dunbar, 1998; Potts, 2002; Grove et al., 2012), and, more specifically, in the study of the initial hominin dispersal into Eurasia (Kingston, 2007; Bar-Yosef and Belfer-Cohen, 2013; Palombo, 2013). The issue has also been central to debates concerning the replacement of Neanderthals by anatomically modern humans (Müller et al., 2011; Barton and Riel-Salvatore, 2012; Stewart and Stringer, 2012). Increasingly detailed palaeoenvironmental reconstructions and better chronological control of both environmental and human fossil data are helping to identify where and when particular regions were suitable for dispersing populations (for a recent review see Palombo, 2013). Kingston (2007) has argued that increases in the quantity and quality of data alone are not likely to help us gain a detailed understanding of hominin adaptive landscapes and of the emergence of global scale evolutionary phenomena. Modelling of dynamic hominin-environment interactions at spatial and temporal scales relevant for both hominin behaviour and evolution can help us make sense of this increasingly abundant and detailed information. Specifically, we have yet to fully investigate the factors that would push or pull hominins into unknown but potentially suitable regions. The explicit connection between mobility decisions made by hominins at the local scale, enabled by increased cognitive complexity, and the emergent pattern of dispersal and replacement at the global scale, has not been explored. Modelling and simulation allow us to study the ways in which global long-term scale phenomena, such as dispersal, emerge from local short-term scale phenomena, such as daily mobility decisions related to foraging.

We seek to address three specific questions in this study. First, how does advanced cognition help hominins navigate and exploit resource landscapes? Second, what effect does environmental heterogeneity have on the natural selection of increased cognition in hominins? Third, how is the dispersibility of a population linked to their cognitive ability? We develop an agent-based model to evaluate the relationship between cognitive complexity, environmental heterogeneity, and hominin dispersal. An agent-based model (ABM) is a computational simulation of autonomous 'agents' that allows us to study the broader scale effects of a large number of local scale individual actions. Agents, which may represent individuals or groups, are programmed to have simple traits and behaviours that may change over time in response to their interaction with the social and physical environment (Rouse and Weeks, 2011). We argue that global scale patterns of dispersal emerge from local scale foraging-based mobility decisions

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rather than some innate or vitalist drive to explore. Specifically, the model tests the effect of foresight on patterns of mobility through heterogeneous resource landscapes. We define foresight as the ability of agents to deliberately and accurately assess and select a preferred environment. The model tests whether this ability could result in increased fitness, whether there is selection for maximum or perfect foresight, and how this selection is affected by environmental heterogeneity. We also discuss how various levels of foresight affect the net directional mobility, or dispersibility, of a population with that ability.

In previous work, we have shown that in some specific types of rapidly changing environments, intermediate rather than maximum levels of foresight are optimal (Xue et al., 2011). In that paper, which used reconstructed temperatures from the Vostok ice core for the last 400 000 years as a proxy for environmental change, but did not deal with a spatial environment, the model found that agents who tracked environmental change too closely during periods of slow change were at a disadvantage during rapid reversals. Agents who were slightly worse at evaluating and tracking the environment were fitter in the long-term and were less adversely affected by climate reversals (Xue et al., 2011). The current paper explores the role of foresight in a spatially complex, or heterogeneous, resource landscape using an agent-based model and demonstrates that intermediate rather than perfect foresight is also optimal in a spatial context. If we assume that high levels of foresight have an associated energetic cost, from increased demands on cognition, our results suggest that the cost would only be paid when specific environments require it.

Palaeoenvironmental reconstructions tell us where and when the doors to dispersal were open and hominin fossils and artefacts provide ‘road-signs’ telling us where and when hominins arrived (Bar-Yosef and Belfer-Cohen, 2013). In this research, we explore how increased cognitive capacity in the form of spatial foresight could have enabled or inhibited hominins from dispersing. Over the course of human evolution, resource availability could have functioned as a powerful but variable ‘pull’ mechanism, shaping dispersal patterns into novel environments, but its impact will have been mitigated by the level of foresight (cognitive ability) that hominins had developed. In short, high levels of environmental heterogeneity might have selected for increased foresight and high levels of foresight might have effectively reduced dispersibility. This suggests that cognitively complex hominins in heterogeneous environments might have had low dispersibility relative to cognitively less complex organisms in more homogeneous environments. Taking this one step further, the model predicts that the environments leading up to major episodes of dispersal, such as the initial hominin dispersal into Eurasia, were likely relatively low in spatial heterogeneity and that the dispersing hominins had relatively low foresight.

Modelling dispersal

In order to study the role of foresight as hominin populations move through landscapes, we must understand how populations disperse through space. Population dispersal is an enigmatic phenomenon. Despite the fact that population dispersal is responsible for broad-scale spatial patterning in the archaeological record, there is little direct evidence of how it occurs. The instances of human populations dispersing into unoccupied territory within recorded history are essentially zero, and documented instances of populations moving into sparsely or variably occupied territory are very few (Kelly, 2003). We are left trying to predict the types of behavioural patterns that would result in dispersal, and then characterizing the spatial patterns this would create in the archaeological and genetic records. The prevalent strategies for modelling dispersal discussed below rely on different assumptions about the importance of demographics, environment, social networks, and especially the importance and scale of environmental knowledge. We discuss approaches from archaeology when available, and introduce useful approaches from other disciplines, particularly ecology, where needed. A brief survey of the main approaches to modelling mobility, environments, and agents and their application to hominin dispersals will help set the stage for the description of our model.

Wave of advance

Ammerman and Cavalli-Sforza (1971) introduced the wave of advance approach in their study of the spread of Neolithic agriculture across Europe. It has since been applied to the Middle to Upper Palaeolithic transition (Bocquet-Appel and Demars, 2000; Davies, 2001; Mellars, 2006a), and the colonization of the New World (Steele et al., 1998; Hamilton and Buchanan, 2007). These studies estimate how fast populations can grow and spread, and how early we could expect the wave to arrive in a given location. Several studies based on Fisher’s (1937) wave of advance equation (Ammerman and Cavalli-Sforza, 1973) or Reaction-Diffusion models (Steele, 2009) focused on the parameter values for the following equations:

$$\frac{\partial n}{\partial t} = \alpha n\left(1 - \frac{n}{K}\right) + D\nabla^2 n \tag{1}$$

and

$$v = 2\sqrt{D\alpha} \tag{2}$$

where K is carrying capacity, α is intrinsic maximum population growth, D is a diffusion distance constant, n denotes population size at a given time, t, and spatial location, and v is wave speed (Steele, 2009). Equation (1) consists of two terms, the first a logistic population growth, and the second a diffusion of that population evenly into the surrounding two-dimensional space. Steele et al. (1998) used values obtained from ethnographic and archaeological literature. These were applied to the Palaeoindian colonization of North American by looking at both the speed of the colonizing wave front and the spatial distribution of resulting populations assuming different rates of population growth, α, and intergenerational movement distance, D.

Wave of advance models generally assume that population growth fills the landscape to carrying capacity and that the movement from dense population centres is random in direction. Neither assumption is necessarily warranted (Meltzer, 2003; Rockman, 2003). For example, Hayden (1972) discusses the self-regulation of human populations well below carrying capacity via a variety of social mechanisms. Moreover, it is unlikely that mobility decisions were made by agents who were blind to the resource potential of the surrounding landscape. Hazelwood and Steele (2004) correctly acknowledge that this is a necessary assumption as a first step to examining dispersal, however, it is unclear how this assumption affects the modelled dispersal pattern.

Least-cost path modelling

Anderson and Gillam (2000) first used least-cost path (LCP) modelling to determine likely routes for the colonization of the New World. In this approach, a series of environmental variables in the form of gridded cell values, usually including topographic slope, are compiled to reflect the energetic cost of traversing a landscape. A Geographic Information System (GIS) is then used to compute the