The role of spatial foresight in models of hominin dispersal

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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.

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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.
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:

\[
\frac{\partial n}{\partial t} = a n \left(1 - \frac{n}{K}\right) + D \frac{\partial^2 n}{\partial x^2}
\]  

and

\[
v = 2 \sqrt{D a}
\]

where \(K\) is carrying capacity, \(a\) 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 America by looking at both the speed of the colonizing wave front and the spatial distribution of resulting populations assuming different rates of population growth, \(a\), and inter-generational 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
least-cost path from known start and destination points. The calculation of the ‘friction’ surface determines how the multiple environmental variables affect mobility. More typically, only a digital elevation model is used to derive first slope and then the caloric cost of climbing that slope. This approach generally assumes a complete prior knowledge of the environment and that mobility was consciously directed towards minimizing the total cost of the path, rather than minimizing the cost of each step. Since, in a dispersal context the landscape is not known in advance, Field et al. (2007), in their study of colonization routes into Southern Asia, developed an innovative ‘wandering’ method of computing least-cost paths in 60 km steps. Unlike Anderson and Gillam (2000), this method did not require that final destinations were known in advance, only that incremental destinations in sequential 60 km searches would be selected by the colonizing population.

A path that minimizes the energetic cost of walking through a landscape may be a good estimation of the routing of individuals on small time scales (for a trade network for example), but it is unclear if successive generations would determine their movements in the same way. A steep hill would not be a deterrent over the course of generations if a quality resource was at the top. Field et al. (2007) argued that the high cost areas would be accessed for resources, but would not be major channels of movement. While it is good to locate these preferred channels of movement, the model’s assumption that energetic cost of movement is the primary factor in mobility decisions seems untenable over the inter-generational residential moves being modelled in hominin dispersal contexts.

Representing the environment

The field of ecology has been modelling dispersal processes much longer than archaeology and has developed a much greater variety of models and model assumptions (Johnson and Gaines, 1990). The resource patch is central to ecological theory and influences modelling frameworks. The patch is a homogeneous resource area, usually a food source, with none of that resource occurring in the inter-patch space. Patch-based analytical models focus on the effects of inter-patch distances, patch size, edge hardness, and clustering (e.g., Zollner and Lima, 1999) on dispersal. In a rare archaeological example, Grove (2013) explored the relationship between inter-patch distance and the natural selection of spatial memory.

Patches are useful for mathematical models due to their simplicity, but introduce somewhat artificial boundaries between some environmental zones. A gradual transition in abundance is not well represented by a patch edge, nor is degree of habitat quality. For example, patch distribution models may not be adequate if we assume hominins are interested in several resources in different proportions.

An alternative approach is to model heterogeneous landscapes of habitat suitability or quality, either as continuous variation, or discretely on a fine scale, usually on a grid. This has the advantage of more realistically representing many types of resource landscapes, while still being relatively simple to represent mathematically (Blackwell, 2007). For example, Mitchell and Powell (2004) represent a continuous heterogeneous resource landscape with a grid of cells varying in value from 0 to 1, and Holland et al. (2009) generate simulated continuous landscapes with varying degrees of spatial autocorrelation or clustering.

Archaeological wave of advance and LCP models represent environments as continuous variation (i.e., as carrying capacity and energetic cost, respectively), but derive their values from palaeoenvironmental or topographical variables, rather than generated environments with specific properties. In a simulation study of the evolution of cultural learning in hominins, Lake (2001) generated continuously varying landscapes of net energetic harvesting return ranging from –100 to +100 using a fractal algorithm. Using this method, he produced multiple landscapes for each of three different levels of environmental heterogeneity.

Cellular automata and agent-based models

Cellular automata models are a more basic precursor to ABMs. They consist of a grid of cells which change state, from empty to colonized for example, based on the condition of their neighbouring cells (Mithen and Reed, 2002). As in wave of advance models, archaeological cellular automata models have focused on calculating the earliest arrival dates in a given location. Mithen and Reed (2002), and the related Nikitas and Nikita (2005) and Hughes et al. (2007), used a probabilistic cellular automata to model the dispersal of Homo erectus throughout the Old World using constant probabilities for movement, colonization (fission), and extinction. These models assumed mobility decisions were made irrespective of the environment, although this was a programming choice and not a limitation of the approach per se.

There have been a number of archaeological ABMs published since the 1970s (see reviews in Aldenderfer, 1981, 1991; Costopoulos and Lake, 2010), including several that model hunter-gatherer foraging patterns (e.g., Mithen, 1990). Comparatively few have dealt with dispersal explicitly. Lake (2000) simulated the first colonization of a small island of the coast of Britain using a custom-made ABM. This required a detailed palaeoenvironmental reconstruction to model the distribution of a hypothesized key food resource, hazelnuts. Simulations were run using several hypothesized origin points, and the distribution of simulated lithic assemblages resulting from model runs were compared with the known archaeological record. In a paper demonstrating the potential of ABMs for studying migration, Young (2002) developed a variety of simple models to show how random walks, biased migration, mobility speeds, population growth rates, and inter-group competition could result in complex patterning. He argued that basic models of foragers looking for food could result in large scale population dispersals without invoking “extraordinary circumstances or motivation” (Young, 2002: 157). Of particular relevance to the current study is Young’s model of biased migrations. In this model, agents randomly selected a neighbouring location, and tested if that location offered an improvement. If it did, they were only allowed to move with a specified probability.

Most of the modelling frameworks discussed above have the drawback of not being able to represent evolutionary processes, such as the evolution of foresight, and dispersal through space simultaneously. However, agent-based models are particularly useful for studying the evolution of traits while modelling the underlying environment. The growth of computational power and the maturation of languages and packages specific for ABM (e.g., Netlogo (Wilensky, 1999) or Repast (North et al., 2007)) means that ABMs can look at the relationship of both processes (evolution and dispersal) within a single framework. It is for this reason that we develop an ABM to look at the relationship between spatial environmental heterogeneity, the evolution of foresight, and the dispersibility of hominin populations.

Role of environmental knowledge in dispersal models

In an early review of dispersal models in population ecology, Johnson and Gaines (1990) identified a series of key ‘push’ or ‘pull’ factors affecting dispersal rates and patterns. Some of the factors are incorporated into models used in archaeology such as population growth in wave of advance models and minimizing cost of movement in least-cost path models. Other factors, such as the probability
of surviving a dispersal episode are highly relevant to hominin dispersal, but are extremely difficult to estimate from archaeological data since failed attempts are less likely to be archaeologically visible. Johnson and Gaines (1990) also propose a number of instructive general conclusions about environmental variability. Temporal variability tends to increase dispersal since the local environment will likely become worse. A spatially heterogeneous environment tends to reduce dispersal since any new location is likely worse.

Random directional movement, often from a ‘push’ such as population growth, is the most widely used approach in archaeology. However, Conradt et al. (2003) argued that random movement is costly in terms of survival due to its high probability of failure. Still, forays or reconnaissance trips before movement can increase success by informing dispersers of potential risks and locating resources. Such trips are commonly noted in ethnographic accounts of foraging, including the diary pattern of daily return trips in the classic forager model or logistical information gathering trips in the collector model (Binford, 1980). The volume edited by Whallon et al. (2011) contains numerous examples of information sharing within and between groups, and of the importance of this information for success and survival. This pattern of exploratory migration has also been noted in contemporary ethnographic examples such as the classic study of Mexican migrants from Tzintzuntzan (Kemper, 1977).

The degree of environmental knowledge underlying mobility decisions in wave of advance and least-cost path models represents two ends of a spectrum. The former assumes random movement with no knowledge of the environment and the latter assumes directed movement with global knowledge. Models can vary along an information continuum from random walks (no information) to local information (spatially limited information) to agents with complex cognitive models or ideal-free distribution models (global knowledge) (Lima and Zollner, 1996). Agent-based models may be designed to fall anywhere along this informational continuum, but are particularly suited to local information. For example, Lake (2000) coded agents to learn about resource distributions from individual observations at the local-scale, and additionally to construct a broader collective memory by sharing that information with other agents.

Modelling spatial foresight in a variable environment

Our ABM approach is informed by results obtained from the above studies and includes an explicitly defined representation of space and resource abundance as continuous variables, and the use of information at a local scale when making mobility decisions. The model uses directed movement, or spatial foresight, but with a variable probability of accuracy. This is similar to the approach of Young (2002) discussed above (see Cellular automata and agent-based models). However, we make foresight a heritable trait varying from 0 to 100% accuracy, within a population of constant size. We then examine how the heterogeneity of the resource environment affects the selective pressure for increased or decreased spatial foresight and its implications for dispersal.

Spatial foresight as a mobility mechanism requires two basic assumptions. The first assumption is that hominin groups were able to evaluate the resource potential of their local, or neighbouring, environment. The second is the model’s ‘pull’, that hominin groups made mobility decisions to improve upon the currently available resources, at least some proportion of the time. The first assumption is not onerous; hominins were certainly able to assess resource abundance or quality in surrounding habitats. However, the scale at which a landscape is expected to be expected is relevant. Our model is designed to operate on a spatial grid, where a move to a new grid cell represents a residential move, and the scale may therefore be adapted to a reasonable distance. A small group of hominins could easily be expected to utilize a 5–10 km radius, or catchment, and assess the resource potential of a slightly larger radius (Vita-Finzi and Higgs, 1970; Kelly, 1995). Binford (2001) collated foraging radius measurements for a large number of ethnographic examples to derive an average 8.28 km radius for foragers. He found the average distance between residential camps ranged between approximately 25 km for plant foragers and 43 km for terrestrial animal collectors. For the sake of generality, we have chosen not to parameterize our model to a specific distance. However, it would be consistent with a 10–20 km grid cell and a 30–60 km local assessment area. In the current study, we are more concerned with the effect of environment heterogeneity than a specific spatial scale (see Model resource landscapes and results, below).

The proportion of mobility decisions that may be attributed to our second assumption, that resources acted as a ‘pull’ during mobility decisions (rather than any number of other factors) is difficult to determine from archaeological evidence, but we will explore this question with our model in the next section. For simplicity, our agents are programmed to make mobility decisions based upon resource abundance some proportion of the time, and that other mobility decisions are made without reference to the resource distribution.

Model outline

Our ABM1, constructed using the Netlogo toolkit (Wilensky, 1999), begins with a population of five hundred agents distributed near one corner of a gridded resource landscape (see Model resource landscapes and results, below). Agents have one attribute, foresight, which is the probability that they will correctly assess the environment of their local (9-cell) landscape. Agents begin each run with perfect foresight, although the result is robust to changes in the initial condition. During each time step, the following schedule of events occurs:

1. Each agent differentially reproduces based on the abundance of resources available on its local cell (see Reproduction, below). There is no accumulation of resources.
   a. Offspring inherit their parent’s foresight value with a slight mutation.
   b. A random empty neighbouring cell is chosen for each offspring agent.
   c. If all neighbouring cells are occupied, the offspring agent is removed.
   d. For every placed offspring, one random agent is removed.
2. Each agent’s inherited foresight determines the probability of correctly predicting the highest resource cell of a 9-cell neighbourhood.
   a. If correct, and the highest resource cell is unoccupied, the agent moves to that cell (i.e., the agent has accurately moved to the best available cell).
   b. If incorrect, the agent moves to a random neighbouring cell as long as it is unoccupied (i.e., the agent has mistakenly moved to a suboptimal cell, possibly one worse than the starting point).
   c. In either case, if the selected cell is occupied, the agent stays.

The mean foresight and mean resource values of the agents are logged with the environmental heterogeneity value at the end of each run. Mean foresight represents the culmination of the evolutionary trend of the agent population. Mean resource value represents the agent population’s collective ability to maximize the currently available resources, effectively their final level of adaptive success. Since the summed cell values of all gridred resource

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1 available for download here: http://www.openabm.org/model/3846.
landscapes are equal, mean success measures the permissiveness of each level of heterogeneity.

Reproduction

Agents represent small groups rather than individual hominins. As such, reproduction occurs by asexual fission with a probability determined by the current success of the group. The ratio of the resource abundance of the cell the agent occupies, \( s \), and the resource abundance of the most successful of all agents, \( \max(\{s\}) \), is multiplied by a base reproduction rate, \( r \) held constant at 0.1, to determine their individual probability of reproduction (Equation (3)). Mutation of foresight occurs as a uniform random value with a specified maximum size, held constant at 0.01, to increase or lower the value.

\[
\frac{s}{\max(\{s\})} r
\]

The constant population size allows us to measure the effect of natural selection in the absence of demographic stochasticity. For the evolution of a trait to occur we need only to implement either differential reproduction or removal of agents. We chose to randomly ‘kill’ agents after successful reproductions, rather than removing those with the lowest resource abundance, to avoid doubling the fitness advantage of the resource landscape.

This process is a simplification of the population growth and fission dynamics of hunter-gatherers under the constraint of carrying capacity in either static or dispersal conditions. We assume simply that more abundant resources lead to a higher rate of population growth and group fission, but that a large number of groups in a small area reduces group fission.

Model resource landscapes and results

Cone

Our simulated environment is represented by a 100 × 100 cell grid of environmental resource values ranging from 0 to 100, where 100 is considered the highest resource value. Before experimenting with complex resource landscapes, we first consider a smooth sided resource cone or bull’s eye where resource abundance decreases evenly away from a high centre area.

When the model is run, the high foresight agents cluster around the central area as they all try to maximize the resources available to them, and thus maximize their rate of reproduction. However, on this simple, relatively homogeneous resource landscape, foresight is strongly selected against and rapidly declines to very low levels (median of 14%, Fig. 1).

Heterogeneous environments

We generated 1100 continuously varying gridded resource landscapes using a stochastic fractal algorithm in the r.surf.fractal module of GRASS GIS (GRASS Development Team, 2012). The algorithm generates natural looking continuous landscapes with increasing environmental heterogeneity specified as increasing fractal dimension, ranging between 2 and 3 (n.b. Since fractal dimensions of 2 and 3 cannot be used in the algorithm, we used 2.001 and 2.999 as our least and most heterogeneous landscapes, respectively). We scaled the cell values produced from 0 to 100 for input into the model, such that every value was approximately equal in frequency and the sum of all cells in a landscape was equal irrespective of the degree of heterogeneity. We generated 100 different landscapes for each of the 0.1 increment increases in fractal dimension (Fig. 2).

After 50 000 time steps of the ABM, a duration our experimental runs determined to be generally sufficient to stabilise at a relatively constant value, we took the mean foresight and resource values of all agents to represent the effect and result of natural selection for each of the 1100 heterogeneous landscapes (Fig. 3). For less heterogeneous environments, mean foresight decreases to very low levels (median 24%), replicating our prior observation on the cone. As the degree of heterogeneity increases, the mean foresight level of the population increases to very high levels (median 85%). Since mean fitness is also increased due to differential reproduction, we ran a series of control runs where agents had no spatial foresight ability to differentiate the effect of foresight from reproduction. Mean success of the control runs was lower than those of foresight for all environments.
Discussion

Dynamics of foresight in heterogeneous environments

As the model progresses on the cone-shaped resource landscape, the highest foresight agents move to the center where there is less space available to reproduce due to crowding. Since more space is available to lower foresighted agents around the edges of the cluster, they are more often successful in placing offspring, even though their reproduction rate is lower. In effect, a new resource of available reproductive space is generated and becomes a more important factor than resource value of the cell in the natural selection of foresight. Natural selection is not driven by who is able to acquire the best resources, but by who can reproduce most successfully. This mechanism, that reproductive space is selected over resource value, is replicated on the less heterogeneous landscapes where resource clusters are relatively wide but decrease in value towards the edges.

As the degree of environmental heterogeneity increases, the clusters of agents become smaller and more dispersed and the availability of reproductive space increases overall. Further, foresight inaccuracies are less well tolerated as they more quickly move an agent onto a low resource cell, because of the steeper resource gradients. As a result, the selective pressure against the high foresight agents is mitigated and the mean foresight of the population increases significantly. These results demonstrate that the level of foresight is density-dependent (Hixon and Johnson, 2009) as a function of the degree of clustering of the resources (the level of heterogeneity), because the summed resource abundance was equal for all landscapes in this experiment.

The inverse relationship between success and heterogeneity is due to the decreased clustering of similar resource values in heterogeneous environments. In a highly heterogeneous environment, if an agent makes a few errors and moves a short distance away from a high resource value, its new environment will likely be a much lower resource location. On a less heterogeneous landscape, mistakes are better tolerated as resource values diminish much less quickly with distance.

Heterogeneity is inversely correlated to success even after the level of foresight has been naturally selected for an environment. Interestingly though, for all heterogeneity levels, the agents are generally more successful than in the control runs despite a widely differing level of foresight of the population (Fig. 4). This suggests that a local environmental awareness, what we have called...
foresight, is a remarkably successful behaviour assuming it is sufficiently adapted to the characteristics of the resource landscape.

**Effect of foresight on dispersal**

While these dynamics explain the natural selection of foresight in different environmental patterns, they do not fully explain the relationship of foresight to dispersal. High foresight causes agents to ‘hill-climb’ to the nearest local optimum, a location on the resource landscape where all surrounding cells are lower in value. It also causes them to become stuck on local optima, because they can accurately predict that their entire accessible neighbourhood is worse than their current location and therefore do not move again. Lower foresight allows agents the potential to random-walk into a novel, and potentially higher, resource area. Agents with very low foresight may not realize they have reached a peak and may walk off the peak, resulting in lower resource abundance. This trade-off is well known elsewhere as a part of evolutionary optimization to adaptive or fitness landscapes (Wright, 1932; Fogel, 1994).

Natural selection of intermediate levels of foresight result in a stochastic hill-climbing behaviour that allows agents to strike an appropriate balance between exploration (‘mistakes’) and resource maximization (hill-climbing). If agents did not make mistakes in assessing the local resources, they would become fixed on the first local optimum they encountered even if was relatively low in resource abundance. Other possible stochastic strategies, like randomly choosing from the subset of better neighbouring cells also exist but were not chosen in this model for simplicity. Choosing from the best of the unoccupied cells would perhaps have been slightly more realistic for a rational agent. However, this would have increased computational time and would have crowded resource peaks even more tightly.

**Figure 3.** The ability to correctly predict the local environment, foresight, is selected against in less heterogeneous landscapes. Grey lines represent runs on 10 different generated landscapes, the black line is the median of those runs. a) Low heterogeneity (2.001). b) Medium heterogeneity (2.5). c) High heterogeneity (2.9). d) Each box plot represents the mean foresight value of 500 agents at the end of runs on 100 different simulated landscapes. Dark horizontal lines represent the median, horizontal edges of the boxes represent the 25th and 75th percentiles, top and bottommost horizontal lines represent 1.5 times the inter-quartile distance. Small circles represent outliers.
...sibility depends on a certain level of inaccuracy in mobility decisions based on resource abundance, or the presence of decision making mechanisms not based on resource abundance. This level of inaccuracy varies strongly with environmental heterogeneity, suggesting that we should look to the periods leading up to major dispersal events, not just during the dispersal, to see how the spatial patterning of the environment could have naturally selected hominin populations to have high or low dispersibility. The model predicts that environments with relatively low heterogeneity are required to naturally select a population with the characteristics necessary, i.e., low foresight, to disperse into unknown environments.

The next step in our research agenda is to look at the strength of the effect of foresight by quantifying dispersal rates of populations with varying levels of foresight, and with population growth, and compare this to expected rates of dispersal in other published dispersal models. This will allow us to explore how expected hominin arrival times in different regions would be altered by a population with foresight. Our future work will help us to clarify the apparent contradiction found by this paper, that environmental heterogeneity favours increased cognitive complexity but not dispersibility.

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