Modelling the Neolithic transition in a heterogeneous environment

M.A. Patterson, G.R. Sarson, H.C. Sarson*, A. Shukurov

School of Mathematics and Statistics, Newcastle University, Newcastle upon Tyne, NE1 7RU, UK

1. Introduction

Two main mechanisms are normally considered for the spread of farming and associated traits (e.g. pottery making, sedentary lifestyles) in the Neolithic transition. The first is demic diffusion (Childe, 1925), in which the Mesolithic population is displaced by the invading Neolithic farmers. In this scenario, the farmers move into a region with an indigenous Mesolithic population who do not adopt the new farming technology. Farming can support a much larger population density than hunting and gathering (foraging), so the farming population density increases rapidly to a value much greater than that of the indigenous people. The indigenous population then finds itself squeezed out as more and more of the land is used for farming. This scenario implies genetic and linguistic homogeneity in subsequent times, as the indigenous population is completely overrrun by the encroaching farmers, so that essentially the entire final population of the region can be traced to the same original culture (Cohen, 1992; Gkiasta et al., 2003).

The second mechanism is trait adoption or cultural transition (Whittle, 1996), in which the farming technology is adopted by the indigenous Mesolithic population. When the Neolithic farmers first arrive in the region, some of the indigenous people convert to farming and begin to increase in numbers as a result. As the invading farmers expand into the region, they have to compete with the converts. This may lead to linguistic heterogeneity, as the indigenous populations endure throughout the region (see Gkiasta et al., 2003; Rendine et al., 1986).

Population dynamics models have been successfully used to quantitatively describe the Neolithic transition. The first such model was suggested by Ammerman and Cavalli-Sforza (1973, 1984), simply describing a constant rate of spread of farming populations, through a homogeneous environment, from the Near-East to Western Europe. Since then other authors have attempted to increase the complexity the model by including multiple populations (e.g. Aoki et al., 1996), population pressure and competition (Ackland et al., 2007), enhanced spread on rivers and coastlines (Davison et al., 2006) and other such features.

2. Multi-population models for a homogeneous environment

Aoki et al. (1996) proposed a model for the transition, involving three populations: initial farmers, converted farmers (hunger-gatherers that become farmers), and hunter-gatherers. The governing equations have the form

\[
\begin{align*}
\frac{\partial F}{\partial t} &= D\nabla^2 F + r_F F (1 - \frac{F}{K}), \\
\frac{\partial C}{\partial t} &= D\nabla^2 C + r_C C (1 - \frac{C}{K}) + e(F + C)H, \\
\frac{\partial H}{\partial t} &= D\nabla^2 H + r_H H (1 - \frac{H}{d}) - e(F + C)H, 
\end{align*}
\]

where \( F(x,t) \), \( C(x,t) \) and \( H(x,t) \), functions of position \( x \) and time \( t \), represent the population densities (in individuals per km\(^2\)) of the initial farmers, converted farmers and hunter-gatherers, respectively. \( K \) is the carrying capacity (the maximum population density that can be supported) of the total farming population, \( L \) is the carrying capacity of the hunter-gatherer population, \( e \) is...
a parameter related to the conversion rate of hunter-gatherers to farmers (measured in km$^2$ per year per individual), $r_f$, $r_c$, and $r_H$ are the intrinsic growth rates ($\text{yr}^{-1}$) of the initial farmers, converted farmers, and hunter-gatherers respectively, and $D$ is the diffusivity (km$^2$ yr$^{-1}$) which, for simplicity, is assumed to be constant and the same for all three populations. We note, however, that the hunter-gatherers are likely to be less sedentary than the farmers, so that a greater diffusivity may be appropriate for them.

The terms on the right-hand side of system (1) are of three types. The first term in each equation is a diffusion term, which corresponds to an isotropic spread. The second term in each equation is a growth term, which has the logistic form for all three populations. The third term, present only for the converted farmer and hunter-gatherer populations, is the conversion term.

A similar term is often used in modelling the spread of diseases, of meetings between farmers (of either type) and hunter-gatherers. This models the rate of conversion as being proportional to the number and natural vegetation type can easily be incorporated as soon as they can be quantified. Further complexities to account for variations in climate, soil fertility, and sea level. It will be assumed that the diffusivities, carrying capacities for both foraging and farming populations. There are numerous parameters, so that we here assume that all of these other. However, we are not aware of any suitable estimates of these parameters are, therefore, required for application to a realistic environment, as will now be addressed.

3. Theory

3.1. A multi-population model for a heterogeneous environment

3.1.1. Environmental heterogeneity

Variations in the rate of propagation of farming across a given region are a very plausible consequence of heterogeneities in the environmental conditions across the region, besides other reasons. Such heterogeneities will also cause variations in the carrying capacities for both foraging and farming populations. There are many effects which can contribute to such variations. For example, fertile soil can support a larger farming population than stony mountain ground; and a dry climate can support a much lower population density than a climate with optimum rainfall.

For simplicity, the environmental effects in our model will be associated with a single environmental variable, the altitude above sea level. It will be assumed that the diffusivities, carrying capacities and growth rates decrease monotonically with altitude, as higher environments are generally less suitable for human habitation. Further complexities to account for variations in climate, soil type and natural vegetation type can easily be incorporated as soon as they can be quantified.

The variation is implemented via multiplying the diffusivities, carrying capacities and growth rates with the decreasing functions of altitude $h$, $a_f$ and $a_H$, corresponding to the farming and hunter-gatherer populations respectively,

$$a_f(h) = \frac{1}{2} \left[ 1 - \text{erf} \left( \frac{h - 1000 \text{m}}{500 \text{m}} \right) \right], \quad a_H(h) = \frac{1}{2} \left[ 1 - \text{erf} \left( \frac{h - 1500 \text{m}}{500 \text{m}} \right) \right],$$

where $h$ is the altitude in metres, which, in turn, is function of position $\mathbf{x}$, and erf is the error function.

The forms, which are displayed in Fig. 1, were chosen more or less arbitrarily, with the only requirement that these quantities become negligible above an altitude of 2000 m for farmers and 2500 m for hunter-gatherers. This assumes that hunter-gatherers can survive in less hospitable conditions, whereas farmers have more difficulty adapting their crops to the harsher conditions at high altitudes.

The carrying capacities of farmers and hunter-gatherers at a particular point in space become

$$K = K_1 a_f(h), \quad L = L_1 a_H(h),$$

where $K_1$ and $L_1$ are the (constant) carrying capacities of farmers and hunter-gatherers at sea level. The diffusion coefficients of farmers and hunter-gatherers become $D_f$ and $D_H$:

$$D_f = D_1 a_f(h), \quad D_H = D_1 a_H(h).$$

And the heterogeneous growth rates are similarly given by

$$r_f = r_{f1} a_f(h), \quad r_c = r_{c1} a_f(h), \quad r_H = r_{H1} a_H(h),$$

where subscript 1 denotes the constant background values. We recall that $h$ is a function of position, so all these parameters can now vary in space.

3.1.2. Density-dependent diffusion

In addition to altitude, diffusion is also likely to depend upon the local densities of the three populations, as use of land by any group will exert a pressure on all groups (including itself), which will enhance the diffusive spread. An insightful discussion of the possible forms of such dependence is provided by Cohen (1992). We modify each diffusion coefficient to include extra terms dependent on each of the population densities, which for simplicity we assume to be linear in the population densities:

$$D_i = a_i + \sum_{j=F,C,H} b_{ij} P_j K_j,$$

where $a_i$ and $b_{ij}$ are certain coefficients, $P_i = F, C, H$ are the population densities, and $K_j = K, L$ are the respective carrying capacities.

In general, all the coefficients $a_i$ and $b_{ij}$ will differ from each other. However, we are not aware of any suitable estimates of these parameters, so that we here assume that all of these coefficients are equal to each other. Then, combining this form with
the altitude dependence introduced in Section 3.1, the diffusivities take the form

\[ D_F = D_C = D_{\alpha_F}(h) \left( 1 + \frac{F + C}{K} + \frac{H}{L} \right), \quad D_H = D_{\alpha_H}(h) \left( 1 + \frac{F + C}{K} + \frac{H}{L} \right). \]

(6)

where \( D \) is the background value of the diffusivities given in Table 1 (the same for the farmers and hunter-gatherers), and \( \alpha_F(h) \) and \( \alpha_H(h) \) are the functions of altitude for the farmers and foragers given in Section (3.1.1).

3.1.3. Density-dependent carrying capacity

As any given region provides only limited resources, it is reasonable to assume that the presence of a hunter-gatherer population will affect the carrying capacity of the combined farming population, and vice versa. In terms of the notation introduced above, the virgin-land (initial) carrying capacity of the total farming population is \( K_{0,L} \) and that of the hunter-gatherer population is \( L_{0,H} \). There is ample archaeological evidence that Neolithic farmers were extensively using wildlife resources to supplement their diet (e.g., fish, molluscs, wild plants and animals), so there was some competition for resources with foragers. Conflicts between the two populations can arguably be also modelled in terms of mutually dependent carrying capacities. We consider the carrying capacity of the farmers to be a monotonically decreasing function of the hunter-gatherer population density, with the simple form

\[ K(H) = A + \frac{BH}{H_0 + H}, \]

where \( A \) and \( B \) are certain constants, with \( B < 0 \), and \( H_0 \) is a characteristic density of the hunter-gatherer population. Thus specified, the carrying capacity of the farmers decreases with the population density of the foragers, \( H \), from the unaffected value \( A \) until it approaches its minimum value \( A + B \) when \( H \gg H_0 \). We impose the conditions \( K(0) = K_{0,T} \) to recover the virgin-land value, and \( \lim_{H \to \infty} K(H) = 0 \) to reflect that a very high hunter-gatherer population density can drive a farming population to extinction. These conditions are met for \( A = K_{0,T} \) and \( B = -K_{0,T} \). If the characteristic population density \( H_0 \) is taken to be the virgin-land carrying capacity of hunter-gatherers at sea level, \( L_{1,T} \), then the carrying capacity of the farmers follows as

\[ K = \frac{K_{0,T}L_{1,T}}{L_{1,T} + H}. \]

(7)

Similarly, the hunter-gatherer carrying capacity becomes

\[ L = \frac{K_{1,T}L_{1,T} \alpha_H}{K_{1,T} + F + C}. \]

(8)

3.1.4. Subsistence boundaries

There are regions into which farming has not ever entered, e.g., high mountains such as the Alps or the Himalayas. These regions are surrounded by subsistence boundaries, which are internal boundaries beyond which the corresponding carrying capacity is sharply reduced. In the model described in section 3.1.3, a population can diffuse across such a boundary, but will then simply die off. Cohen (1992) proposed a form of diffusion that decreases with carrying capacity, so that no population flows across a subsistence boundary; this is more reasonable, as people are unlikely to migrate to an inhospitable region. This form gives a reduced tendency to move into regions with a lower carrying capacity; and as the carrying capacity depends upon the environmental conditions, this introduces further environmental heterogeneity into the model. Introducing a similar form of diffusion to system (1) gives

\[ \frac{\partial F}{\partial t} = \frac{1}{K} \nabla \cdot (D_F K \nabla F) + r_{F_T}F \left( 1 - \frac{F + C}{K} \right), \]

(9)

\[ \frac{\partial C}{\partial t} = \frac{1}{K} \nabla \cdot (D_f K \nabla C) + r_{C_T}C \left( 1 - \frac{F + C}{K} \right) + \epsilon(F + C)H, \]

\[ \frac{\partial H}{\partial t} = \frac{1}{L} \nabla \cdot (D_H L \nabla H) + r_{H_T}H \left( 1 - \frac{H}{L} \right) - \epsilon(F + C)H, \]

where \( K, L, D_{fi} \), and \( D_{H} \) have the forms given in Eqs. This form of diffusion differs slightly from that used by Cohen (1992) and Ackland et al. (2007), but we do not believe that this difference significantly affects the results. This model includes all of the modifications to (1) required to add environmental heterogeneity, population competition, and subsistence boundaries to the model. Furthermore, we have modified the diffusion operator as to allow for the inhomogeneous diffusivities.

3.1.5. Model parameters

Typical values for the constant model parameters are given in Table 1. Some of them have been obtained from the interpretation of European data on the spread of farming from a centre in the Levant. However, our intention is to suggest a working multipopulation model applicable to the initial spread of the Neolithic, rather than to develop a model for a specific region. It would be easy to adjust the model parameters as desired whenever needed.

The diffusivity \( D \) adopted here is smaller, by a factor of two, than that used in modelling the spread of the Neolithic in Europe by Davison et al. (2006) and other authors, about 12.5 km² yr⁻¹. The value of \( D \) used here, which is close to that used by Ackland et al. (2007), produces arguably better results for the Indian subcontinent, because the front speed there was relatively slow (see Section 4.4).

As mentioned in section 3.1.2 (and Table 1), we adopt the same values for the diffusivities of farmers and hunter-gatherers; this may be an oversimplification. For example, Fort et al. (2004) suggest mobility values of 1400–3900 km²/generation, which correspond to diffusivities of \( D = 13–36 \) km² yr⁻¹ for hunter-gatherers, two to six times smaller than the value used here for the Neolithic farmers. As a consequence of our taking the two diffusivities equal to each other, i.e., of underestimating the mobility of the foraging population, the size of the area occupied by the foragers may be underestimated.

Very little is known about the rate of conversion of foragers into farmers, denoted here \( e \). In terms of our notation, Ackland et al. (2007) use \( e_{f}L = 5 \times 10^{-4} \) yr⁻¹ (their parameter \( \gamma \)). For \( L = 0.01 \) km², we then obtain the value of \( e \) given in Table 1.

3.2. Propagation fronts in a heterogeneous domain

We illustrate and explore the solutions of the system (9) in an idealised one-dimensional domain, with all the variables depending only on one coordinate, \( x \). For this purpose, the altitude across the domain is taken to vary as

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Value</th>
<th>Dimension</th>
</tr>
</thead>
<tbody>
<tr>
<td>( D_L )</td>
<td>6.25</td>
<td>km² yr⁻¹</td>
</tr>
<tr>
<td>( r_{F_T} )</td>
<td>0.02</td>
<td>yr⁻¹</td>
</tr>
<tr>
<td>( r_{C_T} )</td>
<td>0.02</td>
<td>yr⁻¹</td>
</tr>
<tr>
<td>( r_{H_T} )</td>
<td>0.01</td>
<td>yr⁻¹</td>
</tr>
<tr>
<td>( K )</td>
<td>0.20</td>
<td>km⁻²</td>
</tr>
<tr>
<td>( L_{1,T} )</td>
<td>0.01</td>
<td>km⁻²</td>
</tr>
<tr>
<td>( e )</td>
<td>0.05</td>
<td>km² yr⁻¹</td>
</tr>
</tbody>
</table>
where \( x \) is measured in kilometres, and \( h \) in metres. This function has the form similar to that given in Fig. 1, with the maximum altitude 1500 m at \( x \to -\infty \), and the minimum value of 0 m (i.e. sea level) at \( x \to \infty \), with a smooth transition at \( x = 3520 \text{ km} \) within about 1000 km of that position.

The simulation uses the boundary conditions posed at \( x = 0 \) and \( x = L \):

\[
\frac{\partial F}{\partial x}(0, t) = \frac{\partial C}{\partial x}(0, t) = \frac{\partial H}{\partial x}(0, t) = \frac{\partial C}{\partial x}(L, t) = \frac{\partial H}{\partial x}(L, t) = 0,
\]

i.e., we assume that there is no population flux at the boundaries of the domain (impenetrable boundaries). Boundary conditions of this type can be especially appropriate to the region similar to the Indian subcontinent, where the boundaries are mostly the sea in the west, south east, and the Himalayas on the north.

In the initial state, farmers occupy the local domain, at their local carrying capacity, and the rest of the domain is occupied by hunter-gatherers, at their local carrying capacity:

\[
F(x, 0) = K_1 a_l, C(x, 0) = 0, H(x, 0) = 0 \text{ for } 0 \leq x \leq 704 \text{ km},
\]

\[
F(x, 0) = 0, C(x, 0) = 0, H(x, 0) = L_1 a_l \text{ for } 704 \text{ km} < x \leq 7040 \text{ km}.
\]

A wave of the farming population may then be expected, travelling from left to right. For the homogeneous system of Aoki et al. (1996) with the parameters given in Table 1, the solutions have the form of a wave initially seeded by the invading farmers, but later be carried on by the converts.

Given the topography of Eq. (10), this test corresponds to a situation where farming has first been established in a highland region, and subsequently spreads into a lower lying area. This test was chosen with the application to the Indian subcontinent, in Section 4, in mind, where the first evidence of agriculture is found in Mehrgarh, in the foothills overlooking the Indus valley.

A travelling wave analysis can be performed on this one-dimensional model (e.g., Murray, 2002), as done for the homogeneous model by Aoki et al. (1996). We include this analysis in the Appendix, for the parameter values given in Table 1. In that case, the analysis predicts a wave speed \( U \), varying with the local environment (via \( h \), which varies with \( x \)):

\[
U = 2\sqrt{2D_{aF}(r_C + eL_1 a_h)} - D_{aF} \frac{\partial}{\partial x} \ln \frac{\partial C}{\partial x}.
\]

Our numerical simulations confirm that this propagation speed is indeed obtained. This formula gives a wave speed in the high altitude region (at 1500 m) of less than one tenth of that at sea level, so our heterogeneous model is clearly capable of explaining large regional variations in the wave speed via the differing environmental conditions (Fig. 1).

Fig. 2 illustrates the steady final state developed in the model, after the wave has propagated across the domain. Two distinct sets of behaviour are found, depending upon the altitude (which controls our environmental heterogeneities). In the high altitude region at \( x < 3520 \text{ km} \) in Fig. 2, the initial farmers rapidly die out, and the hunter-gatherers and converted farmers coexist at relatively low densities (in comparison with the lowland regions) since the carrying capacities are smaller at larger altitude. The population densities settle down to a steady state with approximately constant hunter-gatherer and converted-farmer population densities, as described by the steady state (A2d) identified in the Appendix. This type of solution can be relevant to the long-term survival of hunter-gatherer populations in isolated enclaves.

In the low-altitude region, \( x > 3520 \text{ km} \) in Fig. 2, the hunter-gatherers rapidly convert to farming or die out, but the initial and converted farmers can still coexist and interact. Their interaction meets the condition for steady state (A2e), given in the Appendix. No significant population of initial farmers survives there, however: for the parameters chosen, their number density in the lowland region is rather small and they are taken over by the indigenous farming convert population. This feature of the solution strongly depends on the conversion rate \( e \) adopted: smaller values of \( e \) would allow the initial farming population to spread wider.

Thus there are two distinct states adopted by this model in different regions. In the homogeneous model of Aoki et al. (1996), different behaviours occur for different combinations of parameters, depending on the value of the coefficient, \( g = eK/r_h \). Where \( g > 1 \), a steady state exists where the hunter-gatherer population has died out and farmers remain. However, when \( g < 1 \), the model has a steady state with the populations coexisting and both hunters and farmers remain. In our heterogeneous extension of this model, the environmental heterogeneities cause variations in the local values of the model parameters, and thus allow these differing behaviours to occur at different locations within a single model. For the altitude dependence and parameter values used here, \( g < 1 \) at all realistic altitudes, with the population densities varying with altitude. The model can thus naturally explain heterogeneous population distributions and the survival of enclaves of hunter-gatherers. The most important factor that allows the long-term survival of hunter-gatherers in this model is the altitude dependence of the carrying capacities, where the one of the farmers declines with altitude faster than that of the hunter-gatherers.

4. Application to the initial spread of agriculture to the Indian Subcontinent

In this section we describe a preliminary application of our model to the Neolithic transition in the Indian Subcontinent. We briefly compare the model chronology with some published radiocarbon dates, although a more detailed comparison requires a more thorough analysis involving careful selected radiometric and archaeological data.

A Mesolithic population of hunter-gatherers was widespread throughout India approximately 12,000 years before present (BP). At around 10,000 BP, the change to farming technology occurred in the Near- and Middle-East, spreading to the eastern edge of the Baluchistan plateau. The oldest agricultural settlement on the
of the Neolithic transition in the Indian subcontinent. A more recent summary can be found in Bellwood (2005). From the viewpoint of mathematical modelling, it is important to note that the spread was very inhomogeneous and that enclaves of hunter-gatherers have remained, many of which have even survived until present.

The archaeological evidence presented by Misra (2001) clearly confirms that the rate of propagation of the transition was not uniform. For example, the arrival of farming in the Ganga valley was later than in the south-east of India, which is further from the sources of expansion. Tribes of hunter-gatherers still endure in the highland regions, such as the mountains to the east, dramatically behind the wave fronts, albeit with larger densities than in the lowlands.

Our model was applied for the topography for the Indian subcontinent, using the Terrain Base altitude data from the US National Oceanic and Atmospheric Administration (http://www.ngdc.noaa.gov/). The boundaries of the model domain were 60.0° and 100.0° longitude, and 5.0° and 36.0° latitude. Regions of sea were simply excluded by setting $\alpha_F$ and $\alpha_H$ equal to zero where the altitude is less than or equal to zero. The southern Himalayas form a natural barrier in the north of the domain; to prevent the rapid variations in altitude causing instabilities in the simulation, the values of $\alpha_F$ and $\alpha_H$ were also set to zero if the altitude became greater than 3000 m. The model used the environmental parameterisations developed in Section 3, allowing model coefficients to vary from the base values given in Table 1.

An initial population of farmers, at their local carrying capacity, was placed within a region of one degree in radius centred at $67.9^\circ$E, $29.6^\circ$N, close to Mehrgarh. The source of the spread of farming culture from the East is not precisely known, but to generate this second wave of farmers, a similar source for the farming population was placed at $100^\circ$E, $20^\circ$N. Hunter-gatherers existed at their local carrying capacity everywhere else in the domain. That is, the initial conditions were used were

$$F(x, y) = K_1 \alpha_F; \ C(x, y) = 0; \ H(x, y) = 0,$$
$$F(x, y) = K_1 \alpha_F; \ C(x, y) = 0; \ H(x, y) = 0,$$
$$F(x, y) = C(x, y) = 0; \ H(x, y) = L_1 \alpha_H \quad \text{otherwise},$$

where $x$ is the longitude, and $y$ is the latitude in degrees.

A snapshot 2000 years after the start of the simulation, given in Fig. 4, shows the situation shortly after the two waves of farming have met in the north-east of present-day India, just west of the border with Bangladesh. The blue line indicates a border with a region where the carrying capacities for all three populations is zero (sea in the south and mountains in the north). The unoccupied (dark) regions in the north-east and north-west of panels (a) and (b) are at high altitudes where the farmer’s carrying capacity is very small or zero, but hunter-gatherer populations may survive. The combined farming population density is still relatively low there, and the hunter-gatherer density relatively large compared to surrounding regions. The simulated wave front of farmers moving eastward from Mehrgarh roughly maintains the shape shown in Fig. 3, although it does not replicate the rapid advance down the west coast. At this point the southern tip of India is the only area not yet occupied by farmers, in agreement with Fig. 3. The model farming population nevertheless is faster, arriving somewhat early in southern India, compared with the arrival dates suggested in Fig. 3. (2000 years B.P.) ca. 3500–4000 years after the start of the expansion (6000 years B.P.). The modelled expansion from the East is harder to qualify, because of the greater uncertainty in our understanding of the spread of the Neolithic there (Fuller, 2006).

For both waves (the invading farmers and converts), the invading farmer population dominates near to the sources of agriculture used in the model, and its density decreases with distance from these sources. The converted farmers dominate the farming population closer to the wave front which, in Fig. 4, extends roughly east–west near the latitude $15^\circ$ and also along the east coast. That is, the later propagation of the wave of farming is largely due to the converts, corresponding to our expectation for the background parameters in Table 1 (see the Appendix). The hunter-gatherer density drops dramatically behind the wave fronts, albeit with larger densities surviving in the highland regions, such as the mountains to the east, near the border between Burma and China.

The population densities after 5000 years are shown in Fig. 5. By this time, farming has long been established throughout the region, and the population densities behind the wave front have reached an approximately steady state. Sri Lanka, and the other islands in the domain, remain untouched by farming, since our model does
not allow for sea travel. The model could easily be extended to allow for sea travel as in Davison et al. (2006). The initial farmer density remains largest in the vicinity of the two agricultural sources, while the converted farmer density is greatest away from these centres, as in the snapshot after 2000 years. This occurs because, even after 5000 years from the start of the expansion, the distributions of the populations involved have not reached a steady state. The latter is independent of the positions of the sources.

In the later developments of the model, the two farming populations can slowly diffuse away from their original centres, into the regions occupied by the other population, and the two populations effectively compete for their shared net carrying capacity. Here the net effect is for the regions dominated by the converts to expand somewhat, into the regions initially dominated by the original farmers. This can clearly be seen in Fig. 6, which shows which population is dominant in which parts of the domain, after both 2000 and 5000 years. Comparing Figs. 6 to 4 and 5, however, it is apparent that the two population densities are actually very similar at the borders between regions dominated by original famers and by converts; the net population there is actually quite well mixed.

After 5000 years, the hunter-gatherer population density has dropped in almost all areas behind the wave front. In the lowland area between the Himalayas and the Chota Nagpur plateau, in the north of India, the hunter-gatherer density seems to be decaying, possibly to extinction, which is analogous to the behaviour observed in lowland regions in Section 3. In highland areas such as Baluchistan in the west, the mountains on the extreme east of the domain, and the plateaus in the southern peninsula of India, the hunter-gatherer density has fallen, but not as dramatically as in these lowland regions. This also follows the behaviour seen in Section 3, where enclaves of hunter-gatherers survive in highland regions where farming is less competitive. The relatively low farming population present is dominated by converts, rather than...
the original farmers; this is again in accord with our expectations for the form of wave and steady state appropriate for these conditions (see Section 4 and the Appendix).

Fig. 6 confirms that the hunter-gatherers are the dominant population in these highland regions. Comparing Figs. 7 and 4 shows that the regions of higher final hunter-gatherer density correlate well with regions at high altitude, as might be expected. While the modelled high hunter-gatherer densities in the extreme north-western and north-eastern regions show good agreement with the data available (e.g. Misra et al., 2001; Fuller, 2006), the region of high density on the southern peninsula lies too far south; tribal enclaves there are actually observed in the hilly region close to Maharashtra (~19° latitude, ~73° longitude), where the altitude varies rapidly compared to the southern regions. This may imply that strong variability in the altitude, rather than simply high altitudes, determines the suitability of environments for habitation.

Ackland et al. (2007) also applied a three-population model to simulate the spread of the Neolithic in the Indian Subcontinent. Their results are not directly comparable with those presented here, however, as they consider a single wave of advance spreading from the Fertile Crescent in the West. Their model also includes direct competition between the original and converted farming populations, and so does not allow for the gradual gradients in the two farming populations that we obtain in our final state. Instead, their convert population becomes entirely dominant everywhere west of this. The difference between the two models illustrates the degree of arbitrariness in the choice of the effects included into the model and its parameters. We believe that a more definitive mathematical modelling would be both useful and feasible, but it needs to be carefully controlled via detailed comparison with radiometric, archaeological, linguistic and genetic data. We feel that the models available now offer a suitable basis for such a development.

5. Discussion and conclusions

The isochrons obtained from our model in Section 4, showing the heterogeneous spread of farming, are broadly similar to those derived from the archaeological data available to us. The enhanced coastal spread visible in Fig. 3 is not reproduced by the model, but this might simply be remedied by introducing an enhanced coastal diffusion, e.g. as suggested by Davison et al. (2006). Timings are not everywhere in good agreement, but this is hardly surprising since most of the basic parameters we have used (from Table 1) were originally derived to model the Neolithic in Europe, and it may well be that alternative values are more appropriate for the different environmental conditions of India. Future work will pay greater attention to determining more suitable estimates for these parameters.

Nevertheless, the existing model can already help to explain certain properties of the expansion. For example, Misra (2001) relates the predominance of different language families in different regions to the diffusion of Neolithic farmers and their interaction with the indigenous tribes. The dominant languages in the North-West, where the farmers of the West are dominant in the model, are those derived from Sanskrit (e.g. Hindi, Oriya, Bengali). However, throughout the south of the subcontinent (e.g. Karnataka, Andhra Pradesh and beyond) and in higher-altitude regions of the subcontinent, where the indigenous populations survive in our model in the form of converts to farming and hunter-gatherer tribes, languages belonging to the Dravidian family are spoken. In Bihar, Orissa and West Bengal, where the incoming Eastern farmers dominate in the model, languages of the Austro-Asiatic family are spoken. This distribution should be studied in more detail using more recent analyses of the linguistic landscape of India. The possibility of likewise using data on the genetic variations should also be explored. It is a promising feature of our model that it allows for gradients in the densities of original and converted farming populations (as seen in Fig. 5), that might be related to spatial variations in the genetic background. However all genetic evidence should be approached with caution as genetic heterogeneity can be achieved in purely demic diffusion through the phenomenon known as ‘surging’, which is due to genetic drift in expanding populations (Excoffier and Ray, 2008).

Another successful feature of the model is that it explains the survival of tribes of hunter-gatherers in the less hospitable regions of India as part of a steady state solution. This feature is well understood within the model, as seen from the one-dimensional study in Section 4, which can clearly be linked to the analytical results in the Appendix. Future developments may include more realistic environmental heterogeneities, including factors such as the climate, soil fertility and ecology, which would lead to better modelling of the locations of the hunter-gatherer enclaves.

The model includes several additions to the original 3-population model of Aoki et al. (1996), which each change the way the model evolves. The introduction of altitude-dependent carrying capacity, Eq. (2), causes the farmers’ population density to decline as altitude increases (as $a_h$), while the hunter-gatherers remain at higher altitudes, falling away according to the altitude profile of $q_h$. The main effect of adding the altitude dependence of growth rate and diffusivities in Eqs (3) and (4) is a slowing in the propagation of the wave front at high altitudes. The modified diffusivity also causes changes in the shape of the wave front as it passes features in the altitude profile. For example, as the wave front from the east passes...
longitudes around 90° E, it slows considerably in the foothills of the Himalayas, causing the hunter-gatherers to remain in larger numbers for longer, while the farmers continue to travel quickly along the coast. It may be more appropriate for the diffusivity to decrease with altitude, as higher altitudes are more sparsely populated and people must therefore travel further for trade etc. (we are grateful to anonymous referee for this suggestion). If this is the case then the wave front will travel more quickly in the foothills of the Himalayas, again changing its profile.

Adding population density-dependent carrying capacity as in Eqs (7) and (8) reduces the carrying capacity and therefore the population density of all three populations, but it has no significant effect on the speed or shape of the wave front. Introducing density-dependent diffusivity in the form given in Eq. (6) increases the diffusivity and therefore speeds up the propagation of the wave front, however the choice of form was entirely hypothetical.

We believe that the overall effect of these details is only modest, as it is restricted to the relatively unimportant high altitude areas, and they do not affect the global features in our results. However, we find it useful to include these assumptions into the model having in mind future comparisons with detailed radiometric and archaeological evidence. Of course, the model will have to be refined and refined for that purpose."

In the current model, the same diffusion constant was used for both farmers and hunter-gatherers, despite some reasons for expecting a higher value for hunter-gatherers (see Section 3). Davison et al. (2009) adopted $D = U^2/(4\gamma) \approx 90$ km$^2$/yr for hunter-gatherers using the speed of the spread of pottery making in Eastern Europe, $U = 1.6$ km/yr (Dolukhanov et al., 2005; Davison et al. 2009) and the growth rate $\gamma = 0.007$ yr$^{-1}$. This value is 15 times larger than that used here (Table 1), and 7 times larger than the diffusivity usually adopted for the Neolithic farming populations in Western Europe. However, Fort et al. (2004) suggest that, according to the ethnographic data available, the diffusivity of farmers and hunter-gatherers are rather similar (Fort et al., 2004), as assumed here. We also note that the relatively lower values of the diffusivity adopted here as compared to the European data may be a specific feature of the spread of the Neolithic in the Indian subcontinent. If this can be confirmed by future detailed studies, this fact can have interesting implications for the nature of the Neolithic.

Despite its great simplicity, our model demonstrates the viability of an environmentally heterogeneous model of the spread of farming; and our preliminary application to India provides simple explanations for both the broad distribution of Indian language types, and for the survival of hunter-gatherers in some regions. Improved models must rely on better parameterisations of the basic features of our model (cf. the coefficients in Table 1 and the environmental variations of Section 3), and on more detailed comparisons with the most recent archaeological dates (and possibly also with linguistic and genetic data).

Acknowledgements

The authors thank Pavel M. Dolukhanov for many fruitful discussions about the Neolithic, in India and elsewhere. The authors thank the anonymous referee for drawing the work of Excoffier and Ray (2008) to their attention.

Appendix

Using a well-known method, travelling wave solutions of the one-dimensional form of system (9) can be sought assuming that the dependent variables depend on the single variable, $z = x-\nu t$ (Murray, 2002):

$$F(x,t) = F(z), C(x,t) = C(z), \text{and } H(x,t) = H(z).$$

Then a six-dimensional system is obtained with dependent variables $(F, U, C, V, H, W)$, where

$$U = \frac{dF}{dz}, V = \frac{dC}{dz}, W = \frac{dH}{dz}$$

(A1)

This system has six steady states: four existing for any parameter values,

$$(F, U, C, V, H, W) = (0, 0, 0, 0, 0, 0),$$

(A2a)

$$(F, U, C, V, H, W) = (0, 0, 0, 0, 0, 0),$$

(A2b)

$$(F, U, C, V, H, W) = (0, 0, 0, 0, 0, 0),$$

(A2c)

$$(F, U, C, V, H, W) = (0, 0, 0, 0, 0, 0).$$

(A2d)

$$(F, U, C, V, H, W) = (0, 0, 0, 0, 0, 0).$$

(A2e)

$$(F, U, C, V, H, W) = (0, 0, 0, 0, 0, 0).$$

(A2f)

(together with two other fixed points, which only exist for certain values of parameters:

$$(F, U, C, V, H, W) = \left(0, 0, 0, 0, 0, 0\right) \quad \text{for} \quad F + C = K_1 a_F.$$  

(A2e)

$$(F, U, C, V, H, W) = \left(0, 0, 0, 0, 0, 0\right) \quad \text{for} \quad \frac{eK_1 a_F}{H} < 1.$$  

(A2f)

The state (A2a) corresponds to the lack of any population (the trivial solution), whereas (A2b) and (A2c) have hunter-gatherers alone or converted farmers alone; (A2d) describes coexisting populations of hunter-gatherers and converts. The last two steady states only exist for certain combinations of parameters; (A2e) has coexisting invading farmers and converts whose total population density is equal to their carrying capacity, and (A2f) has all three populations in coexistence. In all the steady states, the derivatives (A1) vanish.

For the steady state (A2d), we have

$$\hat{C} = \frac{K_1}{1-\varphi H} (1-\alpha_C + \alpha_H + \varphi_H \varphi_C) \left[1 \pm \sqrt{1+4\frac{\alpha_F (1-\varphi_H) (1-\frac{\varphi_H \varphi_C}{\alpha_C+\alpha_H})}{1-\alpha_C+\alpha_H+\varphi_H \varphi_C}}\right]$$

where $\varphi_H = K_4 a_H e/F_t$, $\varphi_C = L_1 a_C e/R_C$, and

$$\hat{H} = \frac{\varphi_C}{\varphi_R} \left(1 - \frac{\hat{C}}{K_1 \varphi_C}\right).$$

For the steady state (A2f):

$$F^* + C^* = \frac{K_1 a_C}{1+H^*/L_1}.$$  

$$H^* = \frac{1}{2} \left(\chi \pm \sqrt{\chi^2 + 4L_1^2 a_H \left[1 - \frac{\alpha_C \varphi_H}{\alpha_H}\right]}\right)$$

where $\chi = K_1 a_C + L_1 (1-\alpha_H)$.

If the initial conditions from Section 4 are applied (that is, farming is being introduced into a region occupied by hunters), then by design the steady state (A2b) lies in front of any travelling waves that may form. For the parameter values and initial conditions used in Section 4, we expect the phase plane trajectories to approach (A2b) via the subspace spanned by the stable eigenvectors.

Please cite this article in press as: Patterson, M.A., et al., Modelling the Neolithic transition in a heterogeneous environment, J. Archaeol. Sci. (2010), doi:10.1016/j.jas.2010.07.003
where

\[
\kappa = \frac{L_1 \alpha_H e(1 + \frac{\alpha_C}{\alpha_H})}{2D\sigma_H \mu^2 + \left(U + 3D\frac{\partial H}{\partial x}\right)\mu - \gamma_H}
\]

with the eigenvalues

\[
\mu_{\pm} = \frac{1}{4D\sigma_C} \left\{ -U - D\frac{\partial}{\partial x} \ln \left( \frac{\alpha_C}{\alpha_H} \right) \pm \sqrt{U + D\frac{\partial}{\partial x} \ln \left( \frac{\alpha_C}{\alpha_H} \right)^2 - 8D\sigma_C \gamma_C \left( 1 + \frac{\alpha_H}{\alpha_C} \right) } \right\}.
\]

This solution describes a situation where the later propagation of the wave is carried out by converts, rather than by the original farming population. This requires \( U \geq 2\sqrt{2D\sigma_C \left( \gamma_C + eL_1 \alpha_H \right) - D\frac{\partial}{\partial x} \ln \left( \frac{\alpha_C}{\alpha_H} \right) } \) for the eigenvalues and eigenvectors to be real. The numerical simulations find that the farming advances with the minimum possible speed consistent with this constraint,

\[
U = 2\sqrt{2D\sigma_C \left( \gamma_C + eL_1 \alpha_H \right) - D\frac{\partial}{\partial x} \ln \left( \frac{\alpha_C}{\alpha_H} \right) },
\]

as is the norm for problems of this type.

References


