Mathematical models of the Neolithic transition: a review for non-mathematicians

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1. Introduction

This paper surveys the main existing mathematical models of the Neolithic transition. They are presented in their historical context, in a self-contained way, and using as little mathematics as possible. Still, we reproduce all necessary formulae to reach the results reviewed.

Section 2 presents the classical model by Ammerman and Cavalli-Sforza. Some later refinements of their model are surveyed in sections 3 to 6. We also compare the speed predicted by each model to that implied by the archaeological data. Section 7 contains a new derivation of a recent model. Regional variability is discussed in sections 8 and 9 (using archaeological data and mathematical models, respectively). Finally, section 10 is devoted to concluding remarks.

2. The model by Ammerman and Cavalli-Sforza

While working at Fisher's laboratory in Cambridge from 1949 until 1951, Cavalli-Sforza (1990) learnt about Fisher's model. It was initially conceived to describe the spread of advantageous genes (Fisher, 1937), and later applied to biological invasions (Skellman, 1951). Cavalli-Sforza noted that, if the Neolithic transition was not a process of cultural adoption but mainly due to the dispersal of populations, then: (i) Fisher's equation could hold, and (ii) the values of its parameters could be estimated from anthropological data. This was the first mathematical model of the Neolithic transition. Indeed, according to Fisher's model the population front speed (in kilometers per year) is predicted as (Fisher, 1937; Skellman, 1951)

$$c_{\text{predicted}} = 2\sqrt{aD}\,, \qquad (1)$$

where a is called the initial growth rate of the population number (per year) and D is the population diffusion coefficient (in km² per year).

The faster a population reproduces, the higher its value of a will be, and according to Equation (1) the invasion front will spread faster. Similarly, the further away individuals disperse from their parents, the higher the value of D will be and, again, Equation (1) predicts a faster invasion.

Ammerman and Cavalli-Sforza (1971) gathered the archaeological data available and used them to estimate an observed speed of

$$c_{\text{observed}} = 1.0 \pm 0.2 \text{ km/year}. \qquad (2)$$

They also estimated the diffusion coefficient as Ammerman and Cavalli-Sforza (1984)

$$D \approx \frac{<\Delta^2>}{T}, \qquad (3)$$

where $<\Delta^2>$ is the mean of the squared distance Δ^2 moved by individuals in a generation time, T. Finally, Ammerman and Cavalli-Sforza (1984) also found anthropological observations in the literature for human reproduction, mobility and the generation time T. Those anthropological observations yield the characteristic values

$$a = 0.032 \text{ year}^{-1}, \qquad (4)$$

$$<\Delta^2> = 1544 \text{ km}^2, \qquad (5)$$

$$T = 25 \text{ year}. \qquad (6)$$

Using these values in Equations (3) and (1) yields

$$c_{\text{predicted}} = 2.8 \text{ km/year}. \qquad (7)$$

The prediction (7) is much faster than the speed (2) observed from the archaeological record.

The characteristic mobility value (5) was obtained from *individual* mobility data per generation for pre-industrial agriculturalists (Stauder, 1971). Some *mating* data (distances between birthplaces between husbands and wives) yield much lower values of $<\Delta^2>$, and thus of the predicted speed (1) (Ammerman and Cavalli-Sforza, 1984). However, mating data seem inappropriate because derivations of Fisher's model (Okubo and Levin, 2001; Fort and Méndez, 1999) show that $<\Delta^2>$ corresponds to distances Δ moved *per individual* during the generation time T (i.e., distances moved by individuals from their birthplace until the place where they have children).

This theoretical model, proposed by Ammerman and Cavalli-Sforza (1984), was the first mathematical computation of the predicted speed of the Neolithic transition.

3. Fisher's model in two-dimensional space

Equation (3) gives an order-of-magnitude estimation of the diffusion coefficient D. However, its precise value depends on the number of dimensions, as follows:

(i) For a one-dimensional space (e.g., a population of birds dispersing along a coast) (Okubo and Levin, 2001),

$$D = \frac{<\Delta^2>}{2T}; \qquad (8)$$

(ii) For a two-dimensional space (e.g., a population of humans invading Europe) (Fort and Méndez, 1999),

$$D = \frac{<\Delta^2>}{4T}; \qquad (9)$$

(iii) For a three-dimensional space (e.g. a fish population in an ocean),

$$D = \frac{<\Delta^2>}{6T}. \qquad (10)$$

As it might be expected intuitively, D and therefore the invasion speed (1) are lower the higher the number of available dimensions into which the population can disperse.

Using the observed values (5)-(6) in the two-dimensional formula (9) yields

$$D = 386 \frac{km^2}{gen} = 15.44 \frac{km^2}{yr}, \qquad (11)$$

which used into Equation (1) (with the same values of a and T as above) leads to

$$c_{predicted} = 1.4 \, km/year. \qquad (12)$$

This is a more accurate estimation than (7). However, it is still outside the observed range from the archaeological observations quoted in Equation (2), namely 0.8-1.2 km/year (Ammerman and Cavalli-Sforza, 1971).

4. Time-delayed model

A more refined approach (Fort and Méndez, 1999) noted that Fisher's speed (1) does not take into account the fact that newborn children spend some time T with their parents until they become adults and can migrate. If this effect is taken into account, the predicted speed is

$$c_{predicted \, T} = 2 \frac{\sqrt{aD}}{1 + \frac{aT}{2}}, \qquad (13)$$

instead of Fisher's speed (1). Note that if the effect of the dispersive delay is neglected ($T = 0$), Equation (13) reduces to Fisher's speed (1), as it should.

Using the same parameter values as above, the more refined prediction (13) yields a speed of

$$c_{predicted \, T} = 1.0 \, km/year, \qquad (14)$$

which is consistent with the observed range (0.8-1.2 km/year).

5. Mathematical models versus archaeological observations

Figure 1 shows the distances to Jericho (the presumed center of the Neolithic population dispersal) versus the oldest date of archaeological sites, according to the data used by Ammerman and Cavalli-Sforza (1971, 1984). The full line is their fit to the data. The distance-versus-dates and dates-versus-distances regressions (not shown) yield the observed speed quoted in Equation (2), namely 1.0±0.2 km/year (95% confidence interval) (Fort and Méndez, 1999). Each of the three other lines in Figure 1 gives the best fit using the speed predicted by each of the three models above, namely (7), (12) and (14). The values of χ^2 are the errors of the models relative to the data (i.e., the sum of the squared distances). Clearly the prediction of Equation (14) gives a lower error than those from the non-delayed models (7) and (12).
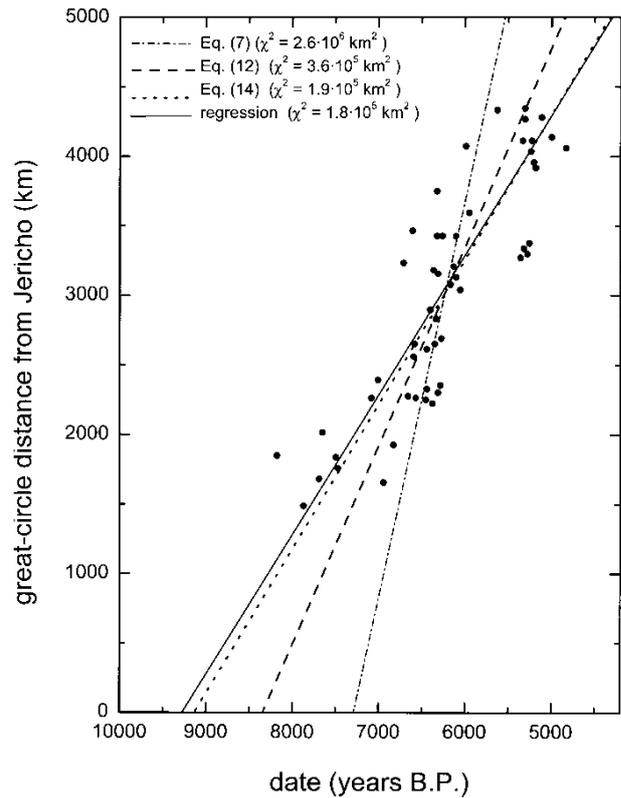

Figure 1. Comparison between observations (from archaeology) and predictions (from mathematical models), after (Fort and Méndez, 1999). The data points (one per archaeological site) and their principal-axis regression are from Ammerman and Cavalli-Sforza (1971, 1984). The time-delayed model, Equation (14), gives a better agreement with the data (i.e., a slower rate of spread) than the non-delayed models corresponding to Equations (7) and (12).
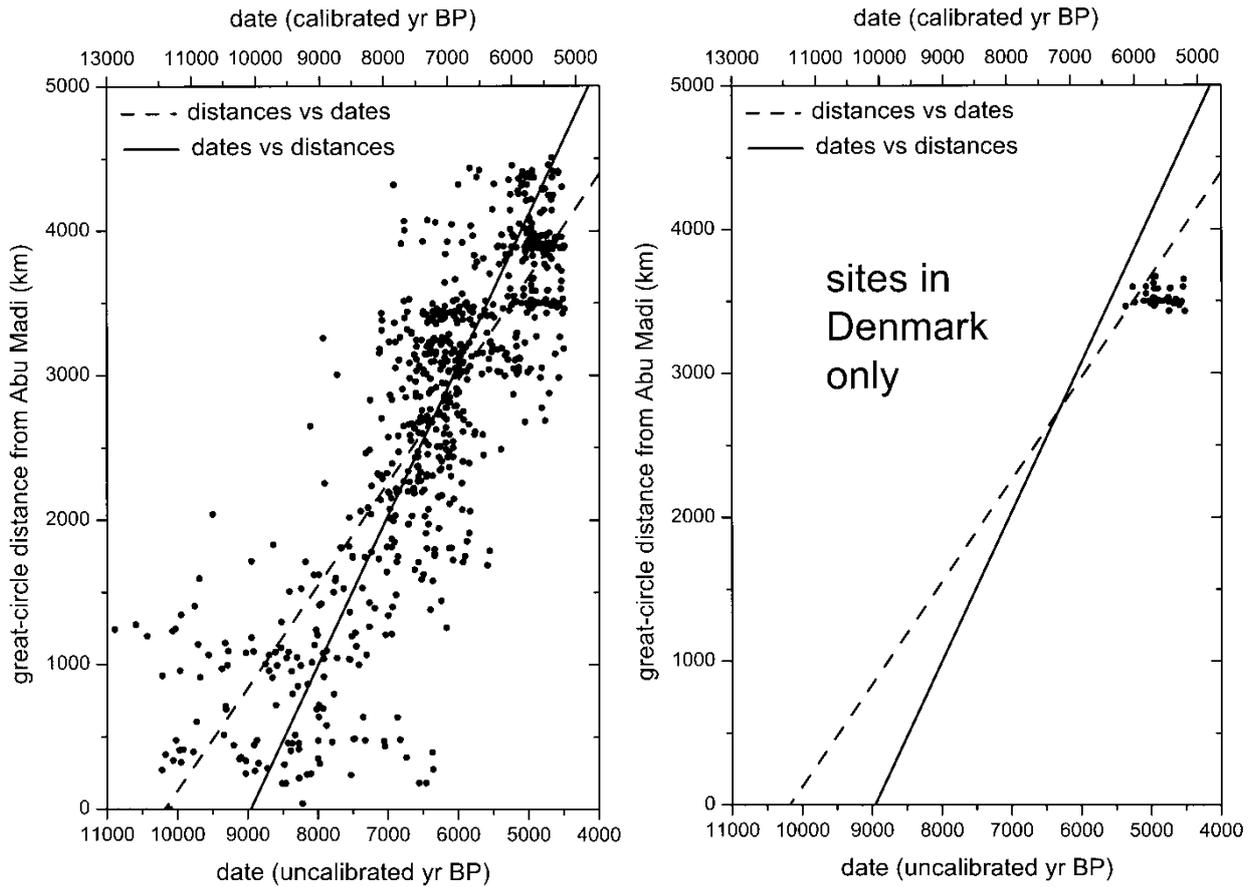
Figure 2. (a) Computation of the speed range using 735 sites, after Pinhasi, Fort and Ammerman (2005). As in Figure 1, great-circle distances have been used. The speed implied by the distance-versus-time regression (dashed line) is its slope, namely 0.71 ± 0.04 km/year. The speed implied by the time-versus-distance regression (full line) is the inverse of the corresponding slope, namely 1.04 ± 0.05 km/year (95% confidence intervals). Therefore, we estimate the overall speed range as 0.7–1.1 km/year. (b) The straight lines are regression fits to 735 sites (the same lines as in Fig. 2.a). However, only sites in Denmark from Fig. 2.a are replotted here (38 data points). A consistent delay shows up in this region, because most sites are to the right (more recent dates) of the regression lines. Further mathematical models are necessary to describe this observation.

A sensitivity analysis using the observed error ranges for the values of the parameters (4)-(6) was also performed, reinforcing the conclusion that the non-delayed models (sections 3 and 4) give speeds too fast compared to the archaeological record (Fort and Méndez, 1999).

As mentioned above, the distance-versus-dates and dates-versus-distances regressions of the 53 sites in Figure 1 lead to an observed speed range of 1.0±0.2 km/year. However, that dataset is now over thirty-five years old (Ammerman and Cavalli-Sforza, 1971). Therefore, it is very important to know if archaeological data available today yield a similar speed range or not. Gkiasta et al. (2003) performed such an analysis with 510 sites and obtained a speed of 1.3 km/year. However, they did not compute an error range for this speed. And they assumed that Jericho was the origin of the dispersal; a different presumed origin will yield a different speed. As stressed by Ammerman and Cavalli-Sforza, the most probable origin should be that which yields a higher correlation

coefficient. Such an analysis has been recently performed for 735 sites (Pinhasi, Fort & Ammerman 2005), and the speed range (using again great-circle distances) is 0.7-1.1 km/year. Again, this range was computed from combining the distance-versus time and the time-versus-distance regressions (Figure 2a). This speed range (0.7-1.1 km/year) can be viewed as a reassuring result, because it is compatible with that obtained by Ammerman and Cavalli-Sforza 35 years earlier (0.8-1.2 km/year). There is no inconsistency and, therefore, this seems to be a sound line of research.

6. Cohabitation models

Let $p(x, y, t)$ stand for the population density (i.e., the number of individuals per unit area centered at the spatial point (x, y) at time t). Fisher's speed (1), as well as its time-delayed generalization (13), can be derived by assuming that, for low values of the population density $p(x, y, t)$,

$$p(x,y,t+T) = R_0 \; p(x,y,t) + \sum \Pi(x',y' \to x,y) \; p(x',y',t) \quad (15)$$

where the net reproductive rate R_0 depends on the initial growth rate a (appearing in Equation (1)) as $R_0 = e^{aT}$ (Fort, Pérez-Losada and Isern, 2007). In the last term, $\Pi(x',y' \to x,y)$ is the net probability than an individual moves from (x',y') to (x,y). The sum Σ indicates that we take into account all possible origins (x',y').

Recently it has been argued that a more realistic model should be the following (Fort, Pérez-Losada and Isern, 2007)

$$p(x,y,t+T) = R_0 \sum \Pi(x',y' \to x,y) \; p(x',y',t) . (16)$$

Similar models are widely used in ecology (Weinberger, 1978; Clark, 1998; Fort, 2007). The difference is that model (15) considers that children appear at the same location as the parents (first term in Equation 15), and parents migrate away from their children (last term). This is not realistic for human populations. In contrast, Equation (16) considers that children grow up with their parents at their final location. Thus Equation (16) is a cohabitation model, whereas (15) is not. The same conceptual limitation applies to Fisher's model (1) and its time-delayed generalization (13), because they are both special cases of the model (15). The differences between the cohabitation model (16) and the model (13) are as large as 30% (Fort, Pérez-Losada and Isern, 2007). However, the speed range predicted by (16) is still consistent with the observed range, namely 0.7-1.1 km/year (from Figure 2a).

7. Dispersive-variability models

In this section we present a new derivation of the cohabitation model, reviewed in the previous subsection. This derivation is motivated by work by other authors showing the importance of taking the age-structure of populations into account in mathematical models (Pinhasi, Fort and Ammerman, 2005), as well as by some recent dispersive-variability models (Harris, 2003; Méndez, Ortega-Cejas and Campos, 2005).

Any human population can be regarded as composed of three sub-populations, with different behaviors: juveniles (e.g., individuals $< \tau$ years old, where τ is the age at first reproduction), reproducing adults (e.g., aged $\geq \tau$ years old and reproducing), and non-reproducing adults (because of age, sterility, or other reasons). Let $p_J(x,y,t)$, $p_A(x,y,t)$ and $p_{AN}(x,y,t)$ stand for the corresponding numbers of individuals per unit area centered at position (x,y) at time t.

Obviously, the number of juveniles appearing per generation should be related to the number of reproducing adults in the preceding generation $p_A(x,y,t)$, not to the total number of individuals, i.e.

$$p(x,y,t) = p_A(x,y,t) + p_J(x,y,t) + p_{AN}(x,y,t) .$$

How can be write down such a relationship mathematically? If we consider (as a useful approximation) a simple, time-averaged model in which all individuals begin to reproduce at once, we can simply write

$$p_J(x',y',t+T_1) = f \; p_A(x',y',t). \quad (17)$$

where f is the population fecundity, and T_1 is the mean age difference between the first and the last child.

In agreement with anthropological observations (Stauder, 1971), let juveniles migrate away from their parents after some mean time T_2. Then,

$$p_A(x,y,t+T_1+T_2) = s \sum \Pi(x',y' \to x,y) \; p_J(x',y',t+T_1), (18)$$

where s is the fraction of juveniles who will become reproducing adults, and $\Pi(x',y' \to x,y)$ is again the jump probability from (x',y') to (x,y).

Of course, more complicated models can be considered. But this simple model is more detailed than those in the previous sections, because here we take into account that the reproductive and dispersive behavior may depend on age (albeit in the simplest possible way). How does the front speed change when considering this more detailed description? Interestingly, it does not change at all! Indeed, using Equation (17) in the right-hand side of Equation (18), and defining $T = T_1 + T_2$, we come to

$$p_A(x,y,t+T) = R_0 \sum \Pi(x',y' \to x,y) \; p_A(x',y',t), (19)$$

where $R_0 = s \; f$. So we obtain again the cohabitation model, given by Equation (16). The only difference is that here the reproducing adult subpopulation $p_A(x,y,t)$ appears, instead of the total population $p(x,y,t)$. But the important point is that the speed of invasion front solutions is the same as for the cohabitation model in the preceding section. This gives further support to the cohabitation model. It also shows that it is always possible to build more complicated mathematical models, but in some cases this does not lead to any new prediction that can be compared to the archeological data. So it does not seem worthwhile complicating the model from the previous section further (in this direction). Instead, a good guide is given by a quote by Albert Einstein: *"Mathematical models should be kept as simple as possible — but not simpler".*

8. Regional variability: archaeological observations

According to the mathematical models reviewed above, the speed of the Neolithic front is a constant. This predicts that all data points in Figure 1 should fall on a straight line. Clearly this is not the case. Some possible reasons are the following:

(i) Errors in the radiocarbon dates and/or the computed distances. The latter can be due to the existence of several independent spatial origins of agriculture (e.g., an origin for wheat, another one for barley, etc.), to the unavailability of some regions for human settlement (seas and high mountains), etc.

(ii) Regional variability in the spread rate. This should show up as most data points (for the region considered) falling either to the right or to the left of the regression (full line in Figure 1). If the spread slows down in a region, sites will be younger than average, and fall on the right of the regression (more recent dates). Conversely, if the spread accelerates in a region, its sites will be older than average and fall to the left of the regression. For example, Ammerman and Cavalli-Sforza (1971) mentioned a definite slowing down of the spread in Scandinavia. Does their observation hold up for the archaeological data available today? To answer this question, in Figure 2b we repeat the same regressions as in Figure 2a, but plot only the 38 sites from Denmark (from the 735 sites in Figure 2a). Clearly, most data points in Figure 2b lie to the right of the regression lines. Therefore, the new data confirm that the spread was indeed slower in Denmark. No mathematical model has so far explained this observation, let alone the value of its delay time in years.

In the next section, we will discuss how regional variability could be included in mathematical models. But before doing so, let us mention that besides the slowing down of the spread in Northern Europe, there are additional archaeological observations of regional variation that deserve attention; e.g. the delay into the Alpine area (Ammerman and Cavalli-Sforza, 1984; Gkiasta et al., 2003), the accelerated spread of the Bandkeramik in central Europe (Ammerman and Cavalli-Sforza, 1971), and the extremely fast spread along the Western Mediterranean (Ammerman and Cavalli-Sforza, 1971; Zilhão, 2001). Interestingly, the latter is similar in speed to the Neolithic expansion in Oceania (Fort, 2003).

9. Regional variability: mathematical models

Regional variability can be due to many possible reasons, such as:

(i) Geographic or climatic barriers. They are a possible explanation for what appears as a 1,000-year halt in the Neolithic spread into Southern Scandinavia, due to a slow shift from hunter-gatherer into farming economics, possibly because of local difficulties in the practice of agriculture (Price, 2003). Such a halt does not appear of purely cultural origin, but ultimately due to geographic factors.

(ii) Cultural effects. Regions of fast acculturation by hunter-gatherers could in principle show a faster spread (and reduce the coexistence time between hunter-gatherers and farmers, which can be estimated from archaeological data). Mathematically, only recently several-population models have described cultural diffusion effects (Ortega-Cejas, Fort and

Méndez, 2006; Ackland et al., 2007; Fort et al., 2008). This is a wide topic that deserves further work.

(iii) Non-homogeneous values of demographic parameters. From a purely mathematical perspective, this may correspond either to human dispersal parameters (diffusion coefficient D, dispersal probability distribution $\Pi(x', y' \rightarrow x, y)$, time interval between subsequent migrations T) or reproductive ones (values of a and R_0). However, we are not aware of any anthropological data backing such suggestions.

(iv) Anisotropic dispersal effects. When the invading population front enters a region unsuitable for agriculture, humans may have a higher tendency to migrate backwards than forwards. There is some anthropological support for this suggestion, because migration data for the human colonization of Northern America in the XIX century are indeed anisotropic. Mathematical models including such effects have been recently proposed (Davison et al., 2006; Fort and Pujol, 2007).

10. Conclusions

We have surveyed the main mathematical models of the Neolithic transition, as well as their comparison to archaeological observations.

Some additional models, e.g. models with several values of the generation time (Fort, Jana and Humet, 2004), have not been reviewed in this paper (mainly because they yield similar results for the predicted spread rate to the models surveyed).

As reviewed in section 8, archaeological data show that regional variations in the spread rate are important. This is an interesting point that deserves further efforts using mathematical models, such as those summarized in section 9.

Acknowledgments

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