Chapter 5
Population Spread and Cultural Transmission in Neolithic Transitions

Joaquim Fort, Neus Isern, Antonieta Jerardino and Bernardo Rondelli

5.1 Introduction

The Neolithic transition in Europe has been analyzed quantitatively since the seminal work by Ammerman and Cavalli-Sforza (1971). Because the oldest Neolithic sites are located in the Near East, Ammerman and Cavalli-Sforza (1971) fitted a straight line to the dates of European sites versus their distances to a Near Eastern site (Jericho). In this way they estimated a speed of about 1 km/y. Later Ammerman and Cavalli-Sforza (1973, 1984) applied a model due to Fisher (1937) to the spread of preindustrial famers. They found that this model predicts a speed of about 1 km/y, i.e. similar to the observed one. This indicates that a process based mainly on demic diffusion (spread of populations) agrees with the archaeological data in Europe. Here we report on models with a more refined description of population spread than Fisher's model (Fort et al. 2007, 2008). We also recall a recent model that incorporates the effect of cultural diffusion, i.e. the spread of ideas (hunter-gatherers becoming farmers) instead of populations (Fort 2012). This demic-cultural model is then compared to the archaeological data on the Neolithic spread in Europe and southern Africa.

J. Fort (✉) · N. Isern
ICREA/Complex Systems Lab and Physics Department,
Universitat de Girona, C/. Mª Aurèlia Capmany 61, 17071 Girona, Catalonia, Spain
e-mail: joaquim.fort@udg.edu

A. Jerardino
CaSEs Research Group, ICREA/Department of Experimental & Health Sciences,
Universitat Pompeu Fabra, Ramon Trias Fargas 25-27, 08005 Barcelona, Spain
e-mail: amsjerardino@gmail.com

B. Rondelli
ICREA/CaSEs Research Group, Department of Archaeology and Anthropology,
Institució Milà i Fontanals, CSIC, C/. Egipcíaques, 15, 08001 Barcelona, Spain
e-mail: bernardorondelli@yahoo.it

J.A. Barceló and F. Del Castillo (eds.), *Simulating Prehistoric and Ancient Worlds*,
Computational Social Sciences, DOI 10.1007/978-3-319-31481-5_5

5.2 Limitations of Fisher's Model

Consider a population of preindustrial farmers, initially located in some region. Assume they can disperse into other regions that are also suitable for farming but initially empty of farmers. The next generations of farmers will, in general, disperse away from their parents. Then Fisher's model predicts that a wave of advance (also called a front) of farmers will form and propagate with the following speed (Fisher 1937)

$$s_F = 2\sqrt{a_N D_N}, \tag{5.1}$$

where a_N is the initial reproduction rate of Neolithic farmers (which is easily related to their net fecundity and generation time) and D_N is the diffusion coefficient of Neolithic farmers (which is easily related to the probability that farmers disperse away from their parents as a function of distance). Equation (5.1) is very useful. Ammerman and Cavalli-Sforza (Ammerman and Cavalli-Sforza 1973, 1984) used observed values for a_N and D_N into Eq. (5.1) and found that Fisher's model predicts a speed of about 1 km/y, i.e. similar to the observed one for the Neolithic transition in Europe. In recent years, Fisher's model has been refined (Fort et al. 2007). Note that Eq. (5.1) predicts that, for a given value of D_N, the speed increases without bound ($s_F \to \infty$) for increasing values of the initial reproduction rate ($a_N \to \infty$). This is counterintuitive because, for a given value of D_N, the dispersal behavior of the population is fixed. Thus individuals can disperse up to some maximum distance, $\Delta_{\max}$. Then we should expect that (no matter how large is a_N) the speed s_F should not be faster than $s_{\max} = \Delta_{\max}/T$, where T is the time interval between two subsequent migrations (mean age difference between parents and their children). An integro-difference cohabitation model solves this problem (Fort et al. 2007, 2008, 2012). Then Eq. (5.1) is replaced by a more complicated and accurate equation that takes into account a set of dispersal distances per generation and their respective probabilities. However Fisher's speed, Eq. (5.1), is very useful as a first approximation. It is even quite accurate for some pre-industrial farming populations. For example, for the Yanomano (Isern et al. 2008) Fisher's speed (1.22 km/y) yields an error of only 6 % relative to the integro-difference cohabitation model (1.30 km/y). In other cases, Fisher's speed is not so accurate. For example, for the Issocongos (Isern et al. 2008) Fisher's speed (0.56 km/y) yields an error of 30 % relative to the integro-difference cohabitation model (0.80 km/y).

5.3 Possible Forms of the Cultural Transmission Term

The demic models above can be extended by including cultural transmission. Then Fisher's speed, Eq. (5.1) is generalized into (Fort 2012)

$$s = 2\sqrt{\left(a_N + \frac{C}{T}\right) D_N}, \tag{5.2}$$

where C is the intensity of cultural transmission (defined as the number of hunter-gatherers converted into farmers per farmer during his/her lifetime, in the leading edge of the front, i.e. a region where the population density of farmers is very low) (Fort 2012). In the absence of cultural transmission ($C = 0$), Eq. (5.2) reduces to Fisher's speed, Eq. (5.1), as it should.

Equation (5.2) and other models with cultural transmission take into account that hunter-gatherers can learn agriculture not only from incoming farmers, but also from converted hunter-gatherers, i.e. former hunter-gatherers that have (partially) become farmers (as well as their descendants).

An integro-difference cohabitation model with cultural transmission leads to a more complicated equation than Eq. (5.2), and generalizes the integro-difference model summarized in the previous section (Fort 2012).

Both demic-cultural models (i.e., Eq. (5.2) and the integro-difference cohabitation model) are based on cultural transmission theory (Cavalli-Sforza and Feldman 1981), which shows that the number of hunter-gatherers converted into farmers per farmer during his/her lifetime is (Fort 2012)

$$\frac{\Delta P_N}{P_N} = \frac{f\, P_P}{P_N + \gamma\, P_P}, \tag{5.3}$$

where P_N and P_P are the population densities of Neolithic farmers and Mesolithic hunter-gatherers, respectively, and f and γ are cultural transmission parameters. In the leading edge of the front ($P_N \approx 0$), Eq. (5.3) becomes

$$\frac{\Delta P_N}{P_N} = C, \tag{5.4}$$

with $C = f/\gamma$.

A comparison to other approaches is of interest here. In Ecology a widely used model is based on Lotka-Volterra equations, which assume that the interaction between two populations (ΔP_N) is proportional to their population densities (Murray 2003),

$$\frac{\Delta P_N}{P_N} = k\, P_P, \tag{5.5}$$

where k is a constant. This model has the problem that $\Delta P_N / P_N \rightarrow \infty$ if $P_P \rightarrow \infty$, which seems inappropriate in cultural transmission, for the following reason. Assume that a farmer converts, e.g., 5 hunter-gatherers during his lifetime ($\Delta P_N / P_N = 5$) if there are $P_P = 10$ hunter-gatherers per unit area. Then Eq. (5.5) predicts that he/she will convert $\Delta P_N / P_N = 50$ hunter-gatherers if there are

$P_P =$ 100 hunter-gatherers per unit area, $\Delta P_N/P_N =$ 500 hunter-gatherers if there are $P_P =$ 1000 hunter-gatherers per unit area, etc. Contrary to this, intuitively we expect that there should be a maximum in the number of hunter-gatherers that a famer can convert during his/her lifetime, i.e. that $\Delta P_N/P_N$ should have a finite limit if $P_P \rightarrow \infty$. This saturation effect is indeed predicted by Eq. (5.3), as shown by Eq. (5.4). Thus we think that Eq. (5.3) is more reasonable than the Lotka-Volterra interaction, Eq. (5.5).

This point has important consequences because for Eq. (5.3) the wave-of-advance speed is independent of the carrying capacity of hunter-gatherers, $P_{P\,\max}$ (see, e.g., Eq. 5.2). In contrast, for the Lotka-Volterra interaction the wave-of-advance speed does depend on $P_{P\,\max}$. For example, if Fisher's model is generalized by including the Lotka-Volterra interaction, the front speed is (Minedez et al. 1999) (see also Murray 2003 for a similar model)

$$s = 2\sqrt{\left(a_N + \frac{k\,P_{P\,\max}}{T}\right) D_N}. \tag{5.6}$$

The point is that, in contrast to Eq. (5.2), Eq. (5.6) depends on $P_{P\,\max}$. The same happens if the integro-difference cohabitation model (which is more precise than Fisher's model) is generalized by including the Lotka-Volterra interaction (Fort et al. 2008). These results are not surprising because in the front leading edge ($P_N \approx 0$, $P_P \approx P_{P\,\max}$) Eq. (5.5) becomes $\Delta P_N/P_N = k\,P_{P\max}$, which depends on $P_{P\,\max}$ (whereas Eq. 5.4 does not).

Finally, some language competition models use population fractions (rather than population densities) and interaction terms with non-linear powers of P_N and P_P (Abrams and Strogatz 2003). We first consider the linear case. In one such model, Eq. (5.5) above is replaced by (Isern and Fort 2014)

$$\frac{\Delta P_N}{P_N} = \frac{\eta\,P_P}{P_N + P_P}, \tag{5.7}$$

with η a constant. Equation (5.7) is a special case of Eq. (5.3), thus the wave-of-advance speed is independent of $P_{P\,\max}$ also in this model (Isern et al. 2014). It can be argued that the complete model in Isern et al. (2014) is useful for modern populations but not for the Neolithic transition, because it assumes the same carrying capacity for both populations. But a model that allows for different carrying capacities (Fort and Pérez-Losada 2012) also leads, in the linear case, to an equation with the form of Eq. (5.7). In conclusion, some models originally devised to describe language competition also lead to the conclusion we have stressed above, namely that the wave-of-advance speed is independent of $P_{P\,\max}$.

For completeness, in the non-linear case the following two limitations of the language-competition models discussed in the previous paragraph (Abrams and Strogatz 2003; Isern et al. 2014; Fort and Pérez-Losada 2012) should be noted in the context of the Neolithic transition.

(i) In the non-linear case, Eq. (5.7) above is generalized into (Isern et al. 2014)

$$\Delta P_N = \frac{\eta P_N^{\alpha} P_P^{\beta}}{(P_N + P_P)^{\alpha+\beta-1}} \tag{5.8}$$

with $\alpha \geq 1$ and $\beta \geq 1$ (Abrams and Strogatz 2003). Thus $\Delta P_N \to 0$ if $P_P \to \infty$, i.e. $\Delta P_N / P_N$ does not have a finite, non-vanishing limit (except in the linear case $\alpha = \beta = 1$, see Eq. (5.6). Alternatively, for the Abrams-Strogatz model in Ref. (Fort and Pérez-Losada 2012), namely

$$\Delta P_N = \kappa \left[\sigma P_P \left(\frac{P_N}{P_N + P_P} \right)^a - (1-\sigma) P_N \left(\frac{P_P}{P_N + P_P} \right)^a \right], \tag{5.9}$$

where $\sigma < 1$ is called the status of language N and $a \geq 1$ is the resistance to language change, we obtain a negative limit for $\Delta P_N / P_N$ if $P_P \to \infty$, which is counterintuitive (Isern et al. 2014) (except again in the linear case, $a = 1$). The main point here is that neither of both non-linear models displays the saturation effect discussed above.

(ii) Whereas Eq. (5.3) was derived from cultural transmission theory, the non-linear models introduced to describe language competition (Abrams and Strogatz 2003; Isern et al. 2014; Fort and Pérez-Losada 2012) (Eqs. 5.8 and 5.9) were not.

The non-linear models given by Eqs. (5.8) and (5.9) compare favorably to observed data in non-spatial linguistic systems (Abrams and Strogatz 2003; Isern et al. 2014), and may be applicable to other modern instances of cultural transmission. Perhaps the effects of mass-media, schools, etc. in modern societies avoid the saturation effect discussed above. Such effects are not included in the cultural transmission theory leading to Eq. (5.3) (Fort 2012).

In any case, due to reasons (i) and (ii) above, for the Neolithic transition we prefer not to apply language-competition non-linear models, Eqs. (5.8) and (5.9), neither the Lotka-Volterra interaction, Eq. (5.5). Instead, we apply cultural transmission theory, Eq. (5.3) (or its frequency-dependent generalizations, which take into account the conformist effect but lead to the same conclusions (Fort 2012)).

We stress that the conclusion that the wave-of-advance speed is independent of the hunter-gatherer population density $P_{P\,\max}$ follows from cultural transmission theory, and is ultimately due to the fact that there should be a maximum number of hunter-gatherers converted to agriculture per farmer (or converted hunter-gatherer) during his/her lifetime (this is the saturation effect discussed above).

5.4 Europe

The integro-difference cohabitation model that refines Eq. (5.2) by taking into account a set of dispersal distances per generation and their respective probabilities (see Sect. 5.2) has been applied to the Neolithic transition in Europe (Fort 2012). The results are reproduced in Fig. 5.1, where the horizontal hatched rectangle is the observed speed range from the archaeological dates, namely 0.9–1.3 km/y (Pinhasi et al. 2005). The vertical hatched rectangle is the observed range for the intensity of cultural transmission C from hunting-gathering into farming, according to ethnographic data (Fort 2012). The upper curve is the maximum predicted speed, i.e. that obtained from the model for the fastest observed reproduction rate of human populations that settled in empty space ($a_N = 0.033$ yr^{-1}) and the lowest observed value for the generation time ($T = 29$ yr). Similarly, the lower curve is the minimum predicted speed, i.e. that obtained from the model for the slowest observed reproduction rate of human populations that settled in empty space ($a_N = 0.023$ yr^{-1}) and the highest observed value for the generation time ($T = 35$ yr). Note that without taking into account the effect of cultural transmission ($C = 0$), the predicted speed is about 0.8 km/y (0.7–0.9 km/y), whereas for consistent values of C the speed increases up to 1.3 km/y. Thus the cultural effect is about 40 % (more precisely, 40 ± 8 % (Fort 2012)).

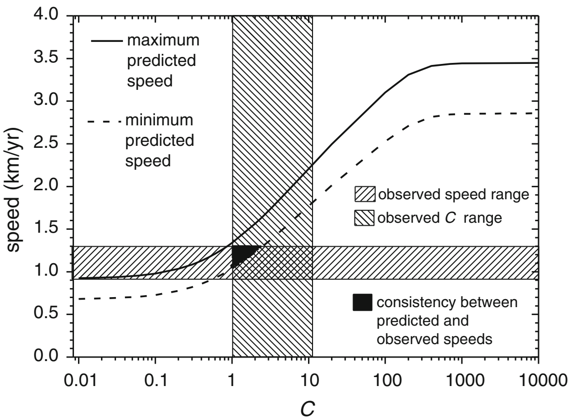

Fig. 5.1 The speed of the Neolithic transition in Europe, as a function of the intensity of cultural transmission C. The horizontal hatched rectangle is the observed speed range of the Neolithic transition in Europe (Pinhasi et al. 2005), and the vertical hatched rectangle is the observed range for the intensity of cultural transmission from hunting-gathering into farming (Pinhasi et al. 2005). Adapted from Ref. (Fort 2012)

5.5 Southern Africa

In southern Africa, the Neolithic transition was a shift from hunting-gathering into herding, not into farming and stockbreeding as in Europe. Another difference is that the speed was 1.4–3.3 km/y (Jerardino et al. 2014), therefore substantially faster than in the European case (previous section). From Fig. 5.1 we thus expect that the value of C (and, therefore, the cultural effect) will be higher in southern Africa than in Europe. This is indeed the case, as we shall now see. Figure 5.2 is the equivalent for southern Africa to Fig. 5.1 for Europe. Thus Fig. 5.2 follows exactly from the same model as Fig. 5.1. The curves are not the same in Figs. 5.1 and 5.2 only because the dispersal kernel (set of dispersal distances and probabilities) used was measured for populations of herders (Fig. 5.2) rather than farmers (Fig. 5.1). The kernel of herders (used in Fig. 5.2) was determined from 4,483 parent-offspring birthplace distances of herders collected by Mehrai (1984). But comparing Figs. 5.1 and 5.2, we note that the waves of advance of farmers and herders are in fact similar. Indeed, the speed obtained without cultural transmission ($C = 0$) is about 1 km/y in both figures, and the fastest possible speed ($C \rightarrow \infty$) is again similar (about 3 km/y). Therefore, as expected, the fastest speed for the southern African Neolithic (1.4–3.3 km/y, horizontal rectangle in Fig. 5.2) as compared to Europe (0.7–0.9 km/y, horizontal rectangle in Fig. 5.1) implies higher values for C in Fig. 5.2 (e.g. $C = 10$) compared to Fig. 5.1 ($C \leq 2.5$, black area in Fig. 5.1). This is why we find that the cultural effect was stronger in the southern African Neolithic. For example, without taking into account the effect of cultural transmission ($C = 0$) the predicted speed is about 1.0 km/y (0.9–1.2 km/y), whereas for ethnographically realistic values of C ($6 \leq C \leq 15$, see Ref. (Jerardino et al. 2014)) the speed

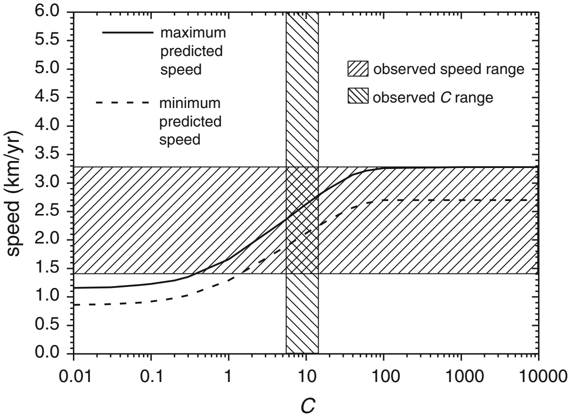

Fig. 5.2 The speed of the Neolithic transition in southern Africa, as a function of the intensity of cultural transmission C. The horizontal hatched rectangle is the observed speed range of the Neolithic transition in southern Africa, and the vertical hatched rectangle is the observed range for the intensity of cultural transmission from hunting-gathering into herding. Adapted from Ref. (Jerardino et al. 2014)

increases up to 2.8 km/y. Thus the cultural effect is about 60 % (more precisely, 57 ± 6 % (Fort 2012)) in southern Africa.

We conclude that the Neolithic transition was mainly demic in Europe (cultural effect about 40 %, i.e. <50 %, see the previous section) but mainly cultural in southern Africa (cultural effect 60 %, i.e. >50 %, as explained in this section). Because the reproductive and dispersal behavior of both populations (farmers in Europe, herders in southern Africa) is likely similar (Jerardino et al. 2014), this difference could be due to a higher ease for hunter-gatherers to learn herding in comparison with farming.

5.6 Conclusion

The European and southern African Neolithic spread are the two first examples in which the percentages of demic and cultural diffusion have been determined. Another interesting example could be the Bantu expansion of farming in Africa (Russell et al. 2014). Many other examples could be studied, provided of course that there were enough data were available to perform statistically sound estimations of the observed speed range. Potential applications include not only Neolithic transitions but also many other spread phenomena of cultural traits, such as the spread of horses in North America (Haines 1938), crop dispersals (Dickau et al. 2007), etc.

Acknowledgment This work was funded in part by ICREA (JF and AJ) and the MINECO grants SimulPast-CSD2010-00034 (all authors) and FIS-2012-31307 (JF and NI). The authors are very thankful to John Kinahan, Jayson Orton, Thembi Russell, Karim Sadr, and Lita Webley for providing useful bibliography.

References

Abrams DM, Strogatz SH (2003) Modelling the dynamics of language death. Nature 424:900
Ammerman AJ, Cavalli-Sforza LL (1971) Measuring the rate of spread of early farming in Europe. Man 6:674–688
Ammerman AJ, Cavalli-Sforza LL (1984) The Neolithic transition and the genetics of populations in Europe. Princeton Univ. Press, Princeton (NJ)
Ammerman AJ, Cavalli-Sforza, LL (1973) A population model for the diffusion of early farming in Europe. In: Renfrew C (ed) The explanation of culture change: models in prehistory. Duckworth, London, pp 343–357
Cavalli-Sforza LL, Feldman M (1981) Cultural transmission and evolution: a quantitative approach. Princeton University Press, Princenton
Dickau R, Ranere AJ, Cooke RG (2007) Starch grain evidence for the preceramic dispersals of maize and root crops into tropical dry and humid forests of Panama. Proc Natl Acad Sci USA 104:3651–3656
Fisher RA (1937) The wave of advance of advantageous genes. Ann. Eugenics 7:355–369

Fort J (2012) Synthesis between demic and cultural diffusion in the Neolithic transition in Europe. Proc Natl Acad Sci USA 109:18669–18673

Fort J, Pérez-Losada J (2012) Front speed of language replacement. Hum Biol 84:755–772

Fort J, Pérez-Losada J, Isern N (2007) Fronts from integrodifference equations and persistence effects on the Neolithic transition. Phys Rev E, 76, paper 031913

Fort J, Pérez-Losada J, Suñol JJ, Escoda L, Massaneda JM (2008) Integro-difference equations for interacting species and the Neolithic transition. New J Phys 24, paper 043045

Haines F (1938) The northward spread of horses among the plains Indians. Amer Anthropol 40:429–437

Isern N, Fort J (2014) Language extinction and linguistic fronts. J Roy Soc Interface, 11, paper 20140028. Eq. (2.6). Equation (7) here corresponds to the linear case, namely $\alpha = \beta = 1$

Isern N, Fort J, Pérez-Losada J (2008) Realistic dispersion kernels applied to cohabitation reaction-dispersion equations. J Stat Mec, 10, paper P10012

Jerardino A, Fort J, Isern N, Rondelli B (2014) Cultural diffusion was the main driving mechanism of the Neolithic transition in southern Africa. PLoS ONE 9:e113672

Mehrai H (2014) A demographic study of some populations in Shahrestan Nowshahr, Mazandaran, Iran, with reference to the genetic structure, 1984, p. 208. Ph.D. Thesis, Durham University. http://etheses.dur.ac.uk/7169/. Accessed 15 Mar 2014

Méndez V, Fort J, Farjas J (1999) Speed of wave-front solutions to hyperbolic reaction-diffusion equations. Phys Rev E 60:5231–5243. Eq. (50)

Murray JD (2003) Mathematical Biology, vol. 2. Springer, Berlin. Eqs. (1.2) and (1.10)

Pinhasi R, Fort J, Ammerman AJ (2005) Tracing the origin and spread of agriculture in Europe. PLoS Biol 3:e410

Russell T, Silva F, Steele J (2014) Modelling the spread of farming in the Bantu-speaking regions of Africa: an archaeology-based phylogeography. PLoS ONE 9:e87854