

Review

Prehistoric spread rates and genetic clines

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Abstract

The seminal book *The Neolithic transition and the genetics of populations in Europe* by Ammerman and Cavalli-Sforza (1984) contains the analysis of archaeological data that led to the result that the spread rate of the Neolithic in Europe was on average about 1 km/yr. It also contains the direct application of a mathematical model that provides an explanation for this value (1 km/yr), the so-called 'wave-of-advance model'. The book also reviews work on the possibility that genetic clines were formed due to the spread of the Neolithic in Europe. This paper is a review of work on both topics since their first joint paper, which was published 50 years ago (Ammerman and Cavalli-Sforza 1971). We also discuss the importance of these and related contributions by Cavalli-Sforza, the present state of the art, and possible lines of future progress.

Based on "Ammerman AJ, Cavalli-Sforza LL. *The Neolithic transition and the genetics of populations in Europe*. New Jersey: Princeton University Press. 1984".

Keywords: spread rates; genetic clines; demic diffusion; cultural diffusion; Neolithic transition

Received: 4 Aug 2021

Accepted: 26 Nov 2021

Published: 6 Apr 2022

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1. A New Field of Research

During his years as a researcher on bacterial genetics in Cambridge (1948–50), Cavalli-Sforza had envisaged the possibility of a totally new field of research that would relate human genes to prehistory [1]. His idea was that as human populations moved around the Earth,

they split many times, so the genetic similarity between present groups could perhaps be used to infer the times and places of the main population movements in prehistory. He made a first attempt in the early 1960s, when he noted that Apulia (a region in the southeast of Italy) and the island of Sardinia have similar megalithic constructions. This similarity suggested that some population capable of constructing them had reached these regions (and other ones in Europe with megalithic monuments). Cavalli-Sforza and his co-workers took blood samples with the hope of finding genetic similarities between the present populations of both regions. However, they could not detect any such similarities [2]. Cavalli-Sforza reasoned that if megalithic populations from outside had arrived and constructed these monuments, they were probably small relative to the populations of farmers already established from long ago. This suggested that only movements of very large populations could perhaps have left genetic traces. Thus his next attempt was to analyze the transition to the Neolithic (farming and stockbreeding), because farmers have substantially higher population densities than the preceding hunting-gathering (Mesolithic) populations [2,3]. It was also known that there are older Neolithic sites in the Near East than in Europe [4,5], but no statistically rigorous analysis of this spread had been performed. At a conference in 1970 [6], Cavalli-Sforza met archaeologist Albert Ammerman, who since 1968 had been collecting early Neolithic dates in Europe [7]. A scant 53 dated sites were then available, since radiocarbon dating had only been developed about two decades before. They plotted the distance of each site from the site in the Near East that yielded the highest correlation coefficient, r , as a function of its date and fitted a straight line. The result is shown in Figure 1a. Their fit had a surprisingly high correlation ($r = 0.89$), suggesting that a constant spread rate was a fairly realistic description of the overall process. Using principal axis regression, they estimated a spread rate (slope) of about 1 km/yr (Figure 1a) [8]. They also considered the regressions of distances vs. dates and vice versa (not shown), which gave a range of 0.8–1.2 km/yr [9]. As mentioned above, these results were obtained using only $n = 53$ sites and published in 1971 [8]. Over the subsequent decades many other sites were dated, and several independent analyses confirmed the spread rate and high correlation estimated by Ammerman and Cavalli-Sforza [8]. For example, in 2005 a study based on 735 sites [10] yielded a similar range (0.7–1.1 km/yr) and correlation coefficient ($r = 0.83$). The corresponding fits are shown in Figure 1b.

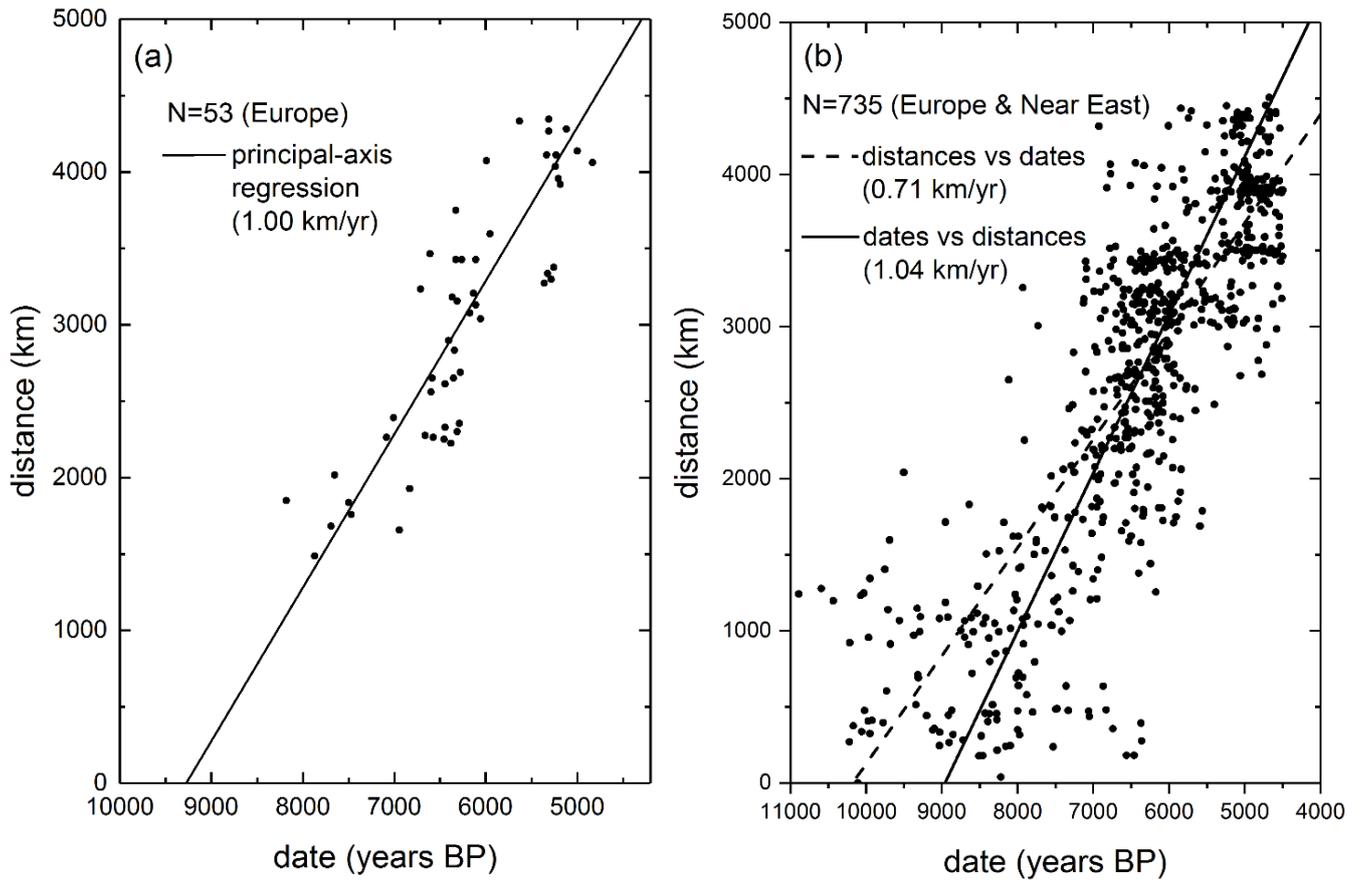


Figure 1 Measuring the spread rate of the Neolithic in Europe. (a) Each dot gives, for one of the N = 53 European sites analyzed by Ammerman and Cavalli-Sforza in 1971 [8,11], its distance from the site of Jericho and its oldest Neolithic date. The line is the principal-axis regression, which was used by Ammerman and Cavalli-Sforza to estimate an average spread rate (slope) of 1.0 km/yr ($r = 0.89$). The regressions of distances vs dates and vice versa (not shown) imply a range for the spread rate of 0.8–1.2 km/yr [9]. Dates are conventional radiocarbon ages in years before present (BP). Each distance is a great circle (*i.e.*, the shortest distance over the surface of the Earth if assumed a sphere) from Jericho, the site that yields the highest value of r (adapted from refs. [9,11]). (b) An analogous analysis that was published 34 years after the pioneering work shown in panel (a). This analysis was based on N = 735 sites in Europe and the Near East [10]. The two regressions (distances vs dates and vice versa) imply a range for the spread rate of 0.7–1.1 km/yr ($r = 0.83$). Distances have been measured along great circles from the site of Abu Madi (the site that yields the highest value of r) (adapted from ref. [10]).

Ammerman and Cavalli-Sforza went further. Also in year 1971, in a congress [12] and a meeting [13] they explored the implications of their spread rate (about 1 km/yr). Cavalli-Sforza knew that Fisher had developed a mathematical (reaction-diffusion) model [14] to describe the spread of an advantageous mutation, which is also useful to describe biological invasions [15]. According to this model, when a population expands its range, the spread rate (*i.e.*, the speed of the population front) is:

$$s = 2\sqrt{aD} \tag{1}$$

which is measured in km/yr . D is the diffusion coefficient, which is defined below and measured in km^2/yr and a is the initial growth rate in yr^{-1} . This means that the population density, p , if small enough, increases with time t as $p = p_0 e^{at}$. Ammerman and Cavalli-Sforza [13] used Equation (1) to estimate the dispersal distance moved by early farmers, in the following way. They applied Fisher's model as originally formulated in one spatial dimension [14], so the diffusion coefficient is given by the one-dimensional expression [16] as:

$$D = \frac{\Delta^2}{2T} \quad (2)$$

where T is the generation time and Δ is the distance moved per individual and generation (for simplicity, we assume for the moment that all individuals move the same distance). Ammerman and Cavalli-Sforza used the spread rate $s = 1 km/yr$ from Figure 1a, an initial growth rate of 3.9% ($a = 0.039 yr^{-1}$) from ethnographic data of human populations that settled in empty space [17], and a generation time of $T = 25 yr$ into Eqs. (1) and (2) and obtained $\Delta \sim 18 km$. In fact, in two dimensions the result is very similar because then Eq. (2) is replaced by [9]:

$$D = \frac{\Delta^2}{4T} \quad (3)$$

and the same procedure as above yields $\Delta \sim 25 km$. Cavalli-Sforza had previously analyzed the movements of individuals of modern and medieval populations using Italian parish books and his own fieldwork in Africa [12,18,19], so he knew that such values for the distance moved per generation Δ are similar to those implied by ethnographic data. This crucial insight has been sometimes overlooked but was very clearly explained by Cavalli-Sforza in a paper at a Genetics congress in year 1971 [12]: "A mathematical theory was put forward by R. A. Fisher (1937) ... As to migration rates, those observed in today's African farmers occupying the tropical forest give ... 20 to 30 km. It is remarkable that, using these growth and migration rates, the expected radial rate comes very close to the observed rate" (*i.e.*, 1 km/yr, as explained above). Thus the direct application of Fisher's spread rate, Eq. (1), was one reason for the proposal by Ammerman and Cavalli-Sforza that the Neolithic spread was mainly due to the dispersal and reproduction of farmers from the Near East.

Cavalli-Sforza came up with the new term 'demic diffusion' [7] (from the Greek *demos*, which means people) to denote the geographic spread of a cultural trait (the Neolithic in this case) due to the dispersal and reproduction of people.

The proposal of demic Neolithic diffusion was a radical one at the time, because many archaeologists advocated for 'cultural diffusion', *i.e.*, a scenario in which the Neolithic would have spread due to the learning by hunter-gatherers of agriculture from nearby farmers [20-25]. But Cavalli-Sforza reasoned that if cultural diffusion had been the main

mechanism at work, it would have probably led to faster spread rates, s , similarly to the introduction of pottery and other cultural innovations that spread faster because they were substantially simpler to learn than farming and stockbreeding [26]; therefore, Fisher's model would not have led to values of Δ in agreement with ethnographic data.

A second, more intuitive reason for Cavalli-Sforza to believe in the importance of demic diffusion was the strong resistance of hunter-gatherers to become farmers that he had observed in his expeditions to Africa [2,12,27]. A third reason was the existence of genetic clines, *i.e.*, spatial variations in the frequency of a genetic marker in modern European populations with an extreme in the Near East, such as those of Rh- and HLA-B8 [2,11,26]. Finally, a fourth reason to introduce the hypothesis of demic diffusion was that Ammerman had noted, in his fieldwork in Italy since 1968, a lack of continuity in stone tools between the Mesolithic and the earliest Neolithic, and that almost none of the open-air settlements of early Neolithic age ever produced any evidence of the Mesolithic [28].

As mentioned above, clines centered in the Near East were observed for some (but not all) genetic markers. Thus, it was convenient to find a method to summarize the spatial variation of many genes. Cavalli-Sforza devoted two years of intense work with physicists Menozzi and Piazza to develop and apply such a method [11]. They discovered that the main pattern (first principal component) of protein gene frequencies in present Europeans has an extreme in the Near East, and published this major finding in the journal *Science* [29], defending that it supported the importance of demic diffusion during the Neolithic spread. Their conclusions agreed with those from maps obtained from HLA and non-HLA alleles separately. Sokal and Menozzi corroborated the existence of gradients without using principal components, by computing spatial correlograms for HLA data along the established paths of the spread of agriculture, and pointed out that such gradients were expected if demic diffusion had played a major role in the spread of the Neolithic [30]. Moreover, Sokal and co-workers reported in *Nature* significant correlations between origin-of-agriculture temporal distances (obtained from archaeological dates) and genetic distances, and argued that this also supported the relevance of demic diffusion [31,32]. The demic diffusion model of Neolithic spread became increasingly accepted among geneticists in the 1980s, and the consensus within the genetics community in the early 1990s was that demic diffusion had been important in the spread of the Neolithic in Europe. However, in the mid-1990s the first datasets of mitochondrial DNA (mtDNA) of modern populations appeared and very old ages were estimated for many mutations. This led some geneticists to propose that the clines might not have been formed during the Neolithic spread but much earlier, when the first modern humans spread into Europe, and therefore that the Neolithic spread

had been essentially cultural [33–35]. Barbujani and co-workers defended demic diffusion against these attacks, pointing out that the age of a mutation can be older than that of the migration of individuals carrying the mutation considered [36–39]. Chikhi and his collaborators analyzed nuclear markers, for which they detected geographic clines [40,41], no evidence of population splits older than the spread of the Neolithic [42], and a westward decrease in their estimation of the proportion of Neolithic genes [43]. They argued that these results supported the importance of demic diffusion (see also refs. [36,44]). All of these findings were based on modern DNA.

As mentioned above, many archaeologists rejected from the start (and during four decades) the importance of demic diffusion in the spread of the Neolithic in Europe [21–25]. Indeed, in 2006 an archaeologist [25] still claimed that 'there was a process of adoption of components of the Neolithic package by the indigenous foraging populations (...). The genetic data point to little genetic input from incomers at the time of the Neolithic [33,45]'. Ancient DNA (aDNA) was then available for early European farmers [45], but not hunter-gatherers. A substantial portion (about 25%) of early farmers displayed a mtDNA haplogroup (N1a) that is almost absent today in Europe, so in 2005 the authors of ref. [45] hypothesized that present Europeans did not descend mainly from early farmers, but from hunter-gatherers who had presumably become farmers through acculturation (cultural diffusion) [45]. Cavalli-Sforza cautioned that this conclusion was not justified [46]. He was shown to be right four years later, when DNA of European hunter-gatherers became available and it turned out that they were extremely different genetically from present Europeans, ruling out the possibility that the latter descend mainly from hunter-gatherers [47]. The implication for N1a was that its frequency decreased during the elapsed millennia until today. It was also noted that most hunter-gatherers displayed U5 or U4 haplogroups (*i.e.*, groups of alleles sharing one or more ancestral mutations), which were absent in early farmers, so the latter must have definitely come from other regions (demic diffusion) [47]. In this way, the importance of demic diffusion in the spread of the Neolithic across most of Europe finally became overwhelmingly accepted in the archaeological and genetics communities. This view had been repeatedly advocated by Cavalli-Sforza, as is clearly seen from the title of his 2002 work 'Demic diffusion as the basic process of human expansions' [26].

In order to avoid confusion, it is important to stress that Ammerman and Cavalli-Sforza repeatedly pointed out that, in addition to demic diffusion, cultural diffusion (interbreeding and/or acculturation) should have also taken place to some extent, and that the combination of cultural and demic diffusion would have led to genetic clines. A particularly intuitive explanation of this point can be found in pp. 82–84 of their 1984 book [11].

Unfortunately, some archaeologists [21,48] and geneticists [49] understood that Ammerman and Cavalli-Sforza were claiming that the Neolithic spread had been totally demic. One possible reason for this confusion may be that Fisher's model, Eq. (1), is indeed totally demic. Ammerman and Cavalli-Sforza had to use Eq. (1) because no cultural-demic generalization of it was then available. For this reason, at the time it was reasonable to use Eq. (1) as an approximation. This point is much easier to explain today because Fisher's equation has been generalized, for cases in which there is cultural in addition to demic diffusion, into (see Eq. (S11) in ref. [50])

$$s = 2\sqrt{\left(a + \frac{\eta}{T}\right)D} \quad (4)$$

where η is the intensity of cultural transmission. If we use the estimation $\eta = 0.02$ (as explained in detail in Sec. 3 below) and the values $a = 0.032 \text{ yr}^{-1}$, $D = 15.44 \text{ km}^2/\text{yr}$ and $T = 25 \text{ yr}$ [9], this equation yields $s = 1.42 \text{ km/yr}$, very close to the totally demic result $s = 1.41 \text{ km/yr}$ from Eq. (1). Thus Fisher's model is indeed valid as a first approximation (more relevant corrections to it are discussed below).

A second important, sometimes overlooked point is that Cavalli-Sforza stressed that the genetic data that he analyzed from modern populations did not make it possible to conclusively quantify the relative importance of demic and cultural diffusion in the spread of the Neolithic in Europe. He did not change his view on this issue, as is very clear from the following text published in year 2002 [26]: "The variance of the first principal component estimate of the Neolithic contribution to Europe is 26–28% [27,29]. Other more recent estimates of the Middle Eastern Neolithic contribution to Europe include those from mtDNA, stated to be 20% [51], and those from the Y chromosome that give a similar estimate (20%) [52]. It seems cautious to think that the data available are still too few and not sufficiently representative ... My view is that we do not yet have really good estimates. I would not be surprised if the contribution of the demic diffusion tied with agriculture should turn out to be greater than 20%. It happens that, with the help of a new method, more advanced than earlier ones, Chikhi *et al.* [43] have just reached the conclusion that the contribution of mid-eastern farmers to Europe is not far from 50%. There are many potential sources of error in the analysis of this problem. We will need better data ...".

A third confusion is that some archaeologists understood that Ammerman and Cavalli-Sforza had advocated for a uniform spread rate over all of Europe [21,22,53], in spite of the fact that already in their first publication they included a list of regions where the spread was faster or slower than average [8].

Ammerman and Cavalli-Sforza presented a more detailed analysis of their demic wave of advance model, based on Eq. (1), in the 1984 book

[11]. Here they used dispersal distances (and therefore, values of the diffusion coefficient) from ethnographic data. Their purpose was to check that they could indeed obtain a spread rate of about 1 km/yr, by using only data estimated from independent observations (*i.e.*, without adjusting any parameter value to obtain a spread rate of about 1 km/yr, as they had done in 1973 with the value $\Delta \sim 18$ km discussed above). They used histograms of several populations. Each histogram is a set of dispersal distances Δ_i moved per generation and their corresponding probabilities, p_i . Then the two-dimensional Equation (3) is generalized into [9]

$$D = \frac{\langle \Delta^2 \rangle}{4T} \quad (5)$$

where $\langle \Delta^2 \rangle = \sum_i p_i \Delta_i^2$ is the mean-squared displacement per generation. In their 1984 book, Ammerman and Cavalli-Sforza applied the approximation

$$D \sim \frac{\langle \Delta^2 \rangle}{T} \quad (6)$$

and they plotted (Figure 5.9 in ref. [11]) the three *lower* curves that we reproduce in Figure 2a. Thus, for each value of the spread rate (0.8, 1.0 and 1.2 km/yr in Figure 2a), a curve gives the pairs of values of a and $\langle \Delta^2 \rangle$ that agree with the spread rate considered according to Eqs. (1) and (6), using again a generation time of $T = 25$ yr. The intuitive meaning of Figure 2a is that for a given spread rate (e.g., the *lower* line for 1 km/yr), if the growth rate a is smaller, then larger dispersal distances $\langle \Delta^2 \rangle$ of the population are needed (and *vice versa*) to attain the spread rate considered. The hatched rectangles in Figure 2a give the ranges of parameters a and $\langle \Delta^2 \rangle$ estimated from ethnographic data of pre-industrial farmers [9]. The three upper curves in Figure 2a use the two-dimensional Eq. (5) instead of the approximation (6). Obviously this leads to a slower spread rate (Eq. (1)), so for given values of s and $\langle \Delta^2 \rangle$ the necessary value of a (for a given rate) is higher, and this is why the three curves for Eq. (5) are above those for Eq. (6) in Figure 2a. The curves for the two-dimensional Eq. (5) are marginally consistent with the measured spread rate (0.8–1.2 km/yr) from Figure 1a. An example of the influence of the work by Ammerman and Cavalli-Sforza on later research is shown in Figure 2b. It was obtained by refining Fisher's model to take into account that newborn humans (farmers in this case) live some time with their parents, and this further slows down the spread rate given by Eq. (1) according to [9]

$$s = \frac{2\sqrt{aD}}{1 + \frac{aT}{2}} \quad (7)$$

The full lines in Figure 2b take this into account, because they have been obtained by using Eq. (7) and (5). It is seen that they agree quite well with the ethnographic data (central rectangle), so the wave-of-advance model is able to explain the average measured spread rate of the Neolithic in Europe.

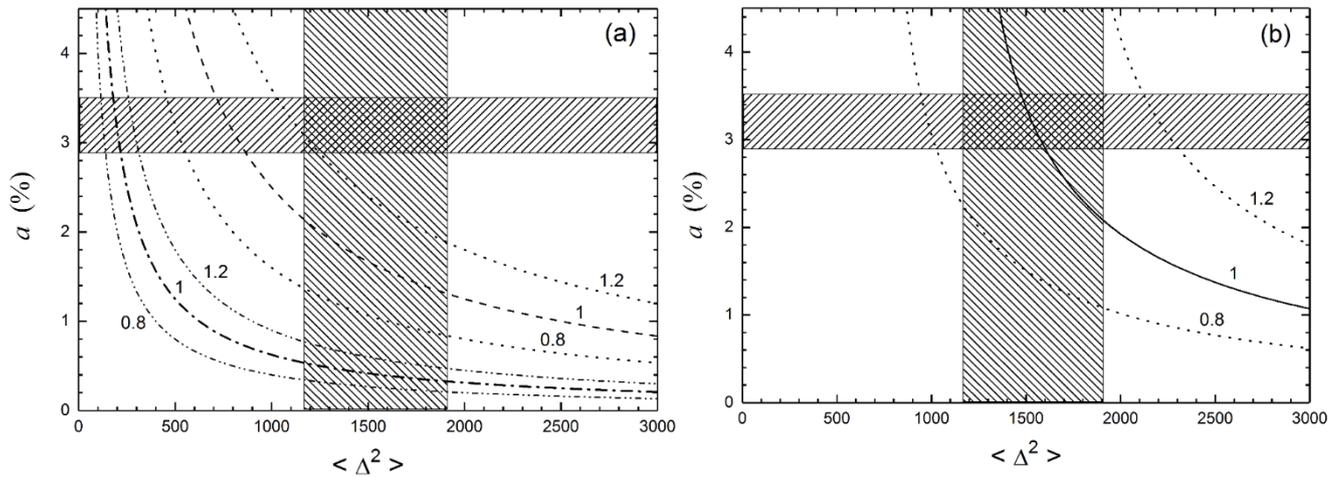


Figure 2 The wave-of-advance model compared to archaeological data. (a) Comparison between the spread rate predicted by Fisher's Equation (1) and the rate measured in Figure 1a (0.8–1.2 km/yr). Each curve is labeled with a number, which gives the spread rate in km/yr. The three lower curves, published by Ammerman and Cavalli-Sforza in their 1984 book as Figure 5.9 [11], have been obtained using the approximate Equation (6). The three upper curves have been plotted using the two-dimensional Eq. (5) [9]. The hatched regions correspond to the ranges of the parameter values according to ethnographic observations. The generation time is $T = 25$ yr (adapted from refs. [9,11]). (b) An analogous analysis published 15 years after the pioneering work depicted in panel (a), using the time-delayed Equation (7) instead of (1) (adapted from ref. [9]).

An alternative way to grasp the difference between Eqs. (1) and (7) is that, as seen above, for the values $a = 0.032 \text{ yr}^{-1}$, $D = 15.44 \text{ km}^2/\text{yr}$ and $T = 25 \text{ yr}$ [9], Eq. (1) yields a spread rate of $s = 1.4 \text{ km/yr}$. In contrast, Eq. (7) yields $s = 1.0 \text{ km/yr}$, which agrees better with the observed rate for the spread of the Neolithic in Europe (0.8–1.2 km/yr, according to Figure 1a). More accurate equations than (7) have been found but they are substantially more complicated [54,109] and it is not necessary to reproduce them here explicitly.

I once asked Cavalli-Sforza if the wave-of-advance model of Neolithic spread had been his idea, and his answer was affirmative (his literal words were “as far as I know”). Cavalli-Sforza wrote [55,56] that he had learned about Fisher's model [14] by perusing Fisher's papers during the two years that he had spent with Fisher in Cambridge (1948–1950). In 1973, more than twenty years later [13], Cavalli-Sforza recalled and applied to Neolithic spread the theoretical model in Fisher's 1937 paper [14], which dealt with a purely genetic issue and already contained the expression 'wave of advance' in its title. Cavalli-Sforza also found it useful [55] that in 1951, Skellman had applied Fisher's paper to a biological invasion [15], and this early application was carefully reviewed in the book written by Ammerman and Cavalli-Sforza in 1984 [11].

My guess is that if Cavalli-Sforza had not worked on this topic, the following sequence of events would have likely happened. (i) During the 1970s or 1980s, some archaeologist would have probably measured

the spread rate of the Neolithic in Europe. (ii) More time would have been necessary for someone to realize that Fisher's wave of advance model could be applied to the spread of the Neolithic in Europe. It is difficult but possible that somebody, e.g., an ecologist interested in archaeology, would have done this during the 1990s or 2000s, but only if he had been familiar with both Skellman's 1951 paper and the Neolithic measured spread rate. (iii) Even today, perhaps nobody could have estimated the necessary parameter values (reproduction rate, generation time and dispersal distances per generation) *from totally independent data* to calculate Fisher's spread rate and compare to the observed value. This was indeed an impressive contribution, and the source of much subsequent work (as reviewed in the next section). In my opinion, very few researchers (if any) besides Cavalli-Sforza had the statistical training and interest in prehistory necessary to perform step (i), the knowledge on both reaction-diffusion partial differential equations [14,15] and Neolithic spread needed to make step (ii), and the research experience in human dispersal behavior [18,19] which, combined with his extraordinary intelligence, allowed him to carry out step (iii). Cavalli-Sforza covered all of these steps in about one year, in collaboration with archaeologist Albert Ammerman (after meeting each other at a conference in the summer of 1970 [6], they begun working together during a visit of Ammerman to Pavia in November of 1970 [7] and reported the measurement of the spread rate in an article published in 1971 [8] and the subsequent application of Fisher's Eq. (1) at a congress in September 1971 [12] and a meeting in December 1971 [13]). This opened a totally new field of research that amazingly joined science and the humanities.

Cavalli-Sforza had interest in many prehistoric spread rates, not only in the European Neolithic. This is very clear from the enthusiasm that he showed with these words [57]: "I have under my eyes an interesting paper (...) The main interest is that it is the only Paleolithic rate that I know". These words led to the first statistically sound measurement of a Paleolithic spread rate [58]. Cavalli-Sforza was also very interested in the possibility of measuring the rates of the Neolithic spread in Austronesia, the Bantu expansion, as well as cultural expansions in hunter-gatherers (he suggested the bow-and-arrow as a very interesting possibility, but unfortunately, we could not find appropriate data to map its spread). His last scientific paper was a review on the out-of-Africa expansion of modern humans [59]. For this case study, unfortunately the archaeological data available today are still not sufficient to perform reliable estimations of the spread rate [60–62,98] but other interesting questions can be tackled. Numerical simulations of the range expansion have been performed by archaeologists, who have analyzed the possible gradual loss of cultural diversity due to drift effects [63]. Cavalli-Sforza and other researchers showed that present genetic diversity decreases linearly with increasing geographic distance

from Africa, and they also detected a very high correlation between genetic and geographic distance (in both cases with $r \approx 0.9$) [64]. They attributed both linear relationships to repeated drift effects, due to small pioneering population sizes during the out-of-Africa expansion (Cavalli-Sforza introduced the term 'serial founder effect' to describe such a process) [64]. Also in his last scientific paper, Cavalli-Sforza and colleagues stressed [59] that the loss of phonemic diversity observed in a worldwide sample of present human languages with increasing distance from Africa [65] could be due to the same serial founder effect. The linguistic processes needed for this proposal to explain the observed phonemic data have been constrained by using wave-of-advance numerical simulations of the out-of-Africa expansion [66,67].

It is worth mentioning that the importance of Neolithic transitions to understanding genetic patterns is not limited to humans. Indeed, simulations taking into account possible consequences of Neolithic spread phenomena on other species have been performed to infer possible scenarios that can explain the observed genetic patterns of European domesticated goats [68] and other domesticated species in several continents [69].

2. Spread Rates of Human Range Expansions and Related Topics

Let us emphasize that Ammerman and Cavalli-Sforza believed in the importance of demic diffusion, but they stated that cultural diffusion also took place. Indeed, already in 1971 they pointed out that the combination of demic and cultural diffusion would have led to genetic clines [8]. On the other hand, Cavalli-Sforza and Feldman [70] carefully distinguished three types of cultural diffusion: vertical, horizontal and oblique. In Neolithic transitions, vertical transmission is interbreeding between farmers and hunter-gatherers. The second type, horizontal transmission, refers to acculturation by farmers of hunter-gatherers of the same generation (who therefore convert into farmers). Finally, oblique transmission describes acculturation by farmers of hunter-gatherers of the preceding generation, and it leads to the fastest spread rates [71].

It was known since 1971 that the observed rate of the Neolithic spread in Europe (Figure 1) agreed with that predicted by Cavalli-Sforza's demic wave-of-advance model (Figure 2) [12,13]. In contrast, no model based on cultural diffusion has been proposed that can explain the observed rate (about 1 km/yr) *using parameter values obtained exclusively from independent observations (i.e., without adjusting any parameter value)* [10].

Ammerman and Cavalli-Sforza applied Fisher's model [12,13]. We emphasize that it is purely demic, *i.e.*, it does not include cultural

transmission. Forty years later [50,72], a refined demic model [54] was combined with the mathematical theory of cultural transmission due to Cavalli-Sforza and Feldman [70]. The resulting demic-cultural model has a crucial parameter η that is called the intensity of cultural transmission. For vertical transmission [72], this parameter η is defined as the portion of pioneering farmers that interbreed with hunter-gatherers [73]. For horizontal transmission, η is defined as the number of hunter-gatherers converted into farmers by each pioneering farmer per generation [50]. If there is both vertical and horizontal transmission, then η is the sum of both contributions, *i.e.*, $\eta = \eta_v + \eta_h$, where the subscripts denote vertical and horizontal transmission. The oblique case is more complicated to handle mathematically (because it involves interactions between different age groups of the two populations) [71], so for simplicity we will not include it here.

The demic-cultural model [50,72] yields an equation according to which the spread rate increases for increasing values of η . We have already seen a very simple equation of this type, namely Eq. (4). Figure 3a is based on a more precise equation [50] that uses the complete dispersal histogram (instead of the diffusion coefficient D , which provides a less detailed description). In Figure 3a, the two curves are the maximum and minimum spread rates obtained for ethnographically realistic ranges of the initial growth rate a and generation time T , as well as a dispersal histogram recorded for pre-industrial farmers in ethnographic fieldwork [12,19]. We see in Figure 3a that for the observed spread rate (horizontal rectangle) to agree with that expected from the model (area between the two curves), it is necessary that $\eta \leq 2.5$ (so only the range of η in the hatched area at the left of Figure 3a and Figure 3b is allowed, namely, $0 \leq \eta \leq 2.5$). This implies that ≤ 2.5 hunter-gatherers were converted into farmers by each pioneering farmer and generation (without interbreeding, *i.e.*, $\eta_v = 0$), or equivalently that ≤ 1.5 hunter-gatherers were converted into farmers by each pioneering farmer and generation (for complete interbreeding, *i.e.*, $\eta_v = 1$).

The effect of demic diffusion on the spread rate is defined as [50]

$$\text{demic effect (\%)} = \frac{s_{\eta=0}}{s} \cdot 100 \tag{8}$$

where s is the spread rate (for the value of η considered) and $s_{\eta=0}$ is the spread rate for purely demic diffusion ($\eta = 0$). The effect of cultural diffusion on the spread rate is defined as [50]

$$\text{cultural effect (\%)} = \frac{s - s_{\eta=0}}{s} \cdot 100 \tag{9}$$

Note that the sum of the demic and cultural effects is always 100%. The cultural effect (9) is plotted in Figure 3b, simply by using the two curves in Figure 3a and Eq. (9). We have seen from Eq. (8) that the maximum possible value of η (from Figure 3a) is $\eta = 2.5$. In Figure 3b, the intersection of the vertical line corresponding to the value $\eta = 2.5$

(right-hand side of the hatched rectangle) with the dashed curve implies that the maximum cultural effect was 48%. Thus the allowed range for η (hatched area at the left of Figure 3b) implies that the cultural effect (9) was between 0% and 48%, *i.e.*, that the demic effect (8) was 52%–100%. This is necessarily higher than 50%, so the conclusion is that demic diffusion had been more important than cultural diffusion in the spread of the Neolithic in Europe [50]. Other dispersal histograms measured for pre-industrial farmers yield still higher ranges of the demic effect (e.g., 70%–100% for the population considered in Figure S1 from ref. [50]).

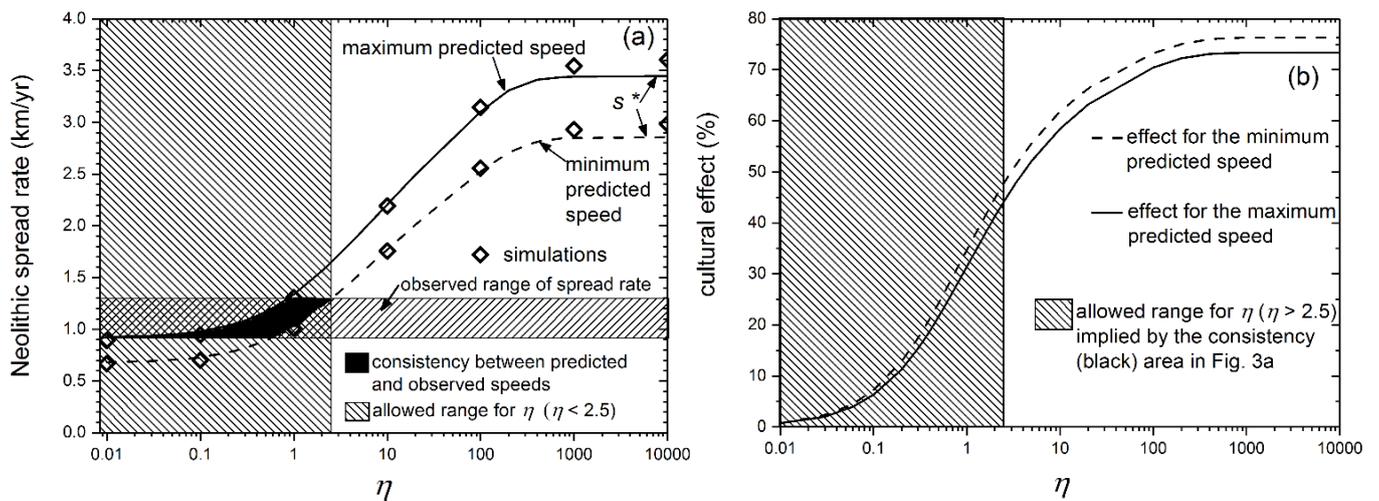


Figure 3 Estimates of the portion η of farmers involved in cultural diffusion and the cultural effect on the spread rate of the Neolithic in Europe. (a) Predicted Neolithic spread rates according to a model that combines demic and cultural diffusion. The horizontal axis is the intensity η of cultural diffusion (so the purely demic model corresponds to $\eta = 0$). The horizontal rectangle is the measured spread rate of the Neolithic in Europe (0.9–1.3 km/yr), which was estimated by applying a more precise approach than that in Figure 1 (namely, linear regressions of dates vs distances, using for the latter separately great circles and shortest paths and considering the overall range [10]). The rhombuses are results of numerical simulations, used to test the analytical results (curves). The upper curve is the maximum speed for the dispersal histogram applied, and was obtained using the highest value for the initial growth rate ($a = 0.033 \text{ yr}^{-1}$) and the lowest value for the generation time ($T = 29 \text{ yr}$) according to ethnographic data. Similarly, the lower curve is the minimum speed, obtained for the lowest initial growth rate ($a = 0.023 \text{ yr}^{-1}$) and highest generation time ($T = 35 \text{ yr}$). For both curves, the same dispersal histogram from a population of pre-industrial farmers (Issongos) was applied. Finally, s^* in the upper right is the maximum possible spread rate, equal to the maximum dispersal distance divided by the generation time. The existence of this maximum s^* is a feature of more refined models [50,54,109] than those based on differential-equations, such as Fisher's. (b) The cultural effect, obtained simply by applying the two curves in panel (a) to Eq. (9). For example, we have applied the values from panel (a) $s_{\eta=0} = 0.92 \text{ km/yr}$ for the upper curve and $s_{\eta=0} = 0.68 \text{ km/yr}$ for the lower one. It is seen from the intersection of the dashed curve with the upper bound for η (vertical line corresponding to $\eta = 2.5$) that the effect on the spread rate is 0%–48%, so the demic effect is 52%–100%.

In the explanation above, we have estimated a minimum percentage of demic diffusion (52%). In principle it is also possible to estimate a maximum percentage [50] but this requires knowing the lower bound of the intensity of cultural transmission η and the ethnographic data from modern populations may not be appropriate, so it is better to use genetic clines instead (see Section 3 below).

The work by Ammerman and Cavalli-Sforza analyzing archaeological data [8,11,13] has led to many further analyses and applications. Gkiasta and co-workers [74] assembled a database of 510 sites, repeated the major-axis regression and found a spread rate of about 1.3 km/yr and $r = 0.73$ (similarly to the results in Figures 1a–b). A different approach was followed by Bocquet-Appel and co-workers, who used geostatistical techniques to estimate the spread rate of several Neolithic cultures of Europe and also found a similar result for the average rate over all of Europe (excluding marine areas), namely 1.1 km/yr [75].

Recently Porcic and co-workers estimated a spread rate for the Neolithic in the central Balkans of 1.6 km/yr using principal-axis regression (the correlation coefficient was remarkably high, $r = 0.81$, given that the maximum distances involved were only about 650 km) [76].

Gkiasta *et al.* produced an isochron map in which a slowdown of the Neolithic wave of advance in alpine regions showed up clearly [74]. This confirmed the existence of a significant slowdown in the Alps, which had been detected in another interpolation map (based only on 62 sites) published in the 1984 book by Ammerman and Cavalli-Sforza [11]. The same slowdown was also displayed with high resolution in an interpolation map based on 918 sites [77]. In Northern Europe, another very clear slowdown was observed [11] and its possible causes included competition for space [78,79], cultural diffusion [77] and climate effects [80].

The effect of waterways on the spread of the Neolithic was analyzed by the group led by A. Shukurov, who estimated spread rates along several coasts and rivers [81] and generalized the mathematical wave-of-advance model to include non-isotropic dispersal [82].

Non-isotropic dispersal has been also proposed as a possible explanation for the fastness of the Khoi-khoi expansion of herders in southern Africa which took place 2,300–1,100 years before the present (BP) at a rate of 1.4–3.3 km/yr and the Bantu expansion of farmers in southeastern Africa which spread at 1.5–2.3 km/yr in the period 3,400–1,400 yr BP [83].

Already in 1971, Ammerman and Cavalli-Sforza had observed that the spread rate of the European Neolithic was faster along the western Mediterranean coast than inland [8]. During the following decades, the number and reliability of dates in that region increased. A particularly

important source of error turned out to be the so-called old wood effect, which is due to the fact that only the outer rings of trees are alive and, therefore, samples of wood or charcoal can lead to erroneously old dates if they correspond to inner rings. For example, at the site of la Draga (Catalonia) the wood of an oak pillar was dated 450 years earlier than some cereal seeds [84]. By taking these and other sources of error into account, Zilhao selected only the most reliable dates in the western Mediterranean and observed that the spread rate was extremely fast [84], although a quantitative estimation was not yet possible [85]. Recently enough data have become available for this purpose, and the result is about 8.7 km/yr, which, combined with simulations based on the wave-of-advance model, implies movements of about 350–450 km per generation along the western Mediterranean coast [86]. Assuming a generation time of 25 years, the rate is $8.7 \text{ km/yr} = 218 \text{ km/gen}$. This is less than 350 km/gen because the latter value could be attained only if reproduction were extremely fast (this is a well-known property of reaction-dispersal equations; see p. 35 in ref. [87]). The estimation of movements with lengths of 350–450 km per generation is based only on data along the western Mediterranean coast of Europe, so it is more precise than previous estimates using data from all of Europe, which already indicated that the dispersal distances per generation along the coast had been longer than inland [88].

Baggaley and co-workers [89,90] applied Bayesian inference techniques to provide improved estimates for several spread rates of the Neolithic in Europe, namely the background spread rate (which corresponds roughly to the average speed of about 1 km/yr found by Ammerman and Cavalli-Sforza [8,11]) and additional coastal and river spread rates (these are relatively small, the coastal one probably because they considered the northern Mediterranean coast as a whole, whereas the fast rate noted by Zilhao refers only to the western coast [84]).

Gagal and co-workers estimated an average spread rate of 0.67 km/yr ($r = 0.87$) for the Neolithic from the Near East across southern Asia, up to the Indus Valley, and suggested that it is slower than in Europe ($\sim 1.0 \text{ km/yr}$) because of the arid climate and complicated topography [91].

Recently de Souza *et al.* [92] fitted the values of six parameters to simulate expansions of forest agriculture in tropical South America and argued that two of them could be successfully modelled as demic waves of advance with realistic parameter values. These are the Saladoid-Barrancoid and the Incised-Punctuate expansions, with average spread rates about 1.3 km/yr ($r = 0.86$) and 1.9 km/yr ($r = 0.91$), respectively (but the corresponding error ranges are substantial, due to the paucity of adequate data) [92]. Very recently they have analyzed the roles of tropical moist forests on the spread of the Tupi (one of the largest language families in South America) using archaeological

data and, in spite of the uncertainties (a few sites are about 3,000 yr older than the rest), they find that the results from the simulations improve substantially if the land cover is assumed to influence human dispersal [93].

Bernabeu and his collaborators simulated the spread of the Neolithic in Iberia under several models (with and without dispersal to non-adjacent grid cells, with and without taking into account the suitability of each cell for wheat farming, *etc.*) and compared to several archaeological databases (the oldest date per site, the most reliable date per site, *etc.*). They concluded that the models that fit the empirical data best are those in which farmers do not always jump to the nearest cells and those in which farmers prefer highest-quality land [94]. They also found that the most reliable databases agreed better with the simulations, so that the quality of the radiocarbon samples needed to be considered [95]. They compared simulations to data using the correlation coefficient of the linear fit between simulated and observed dates. It would be of interest to consider also the sum of the squares of the differences between simulated and observed dates.

Conolly *et al.* [96] found a decrease in the diversity of cereals and pulses in central Europe compared with southeastern Europe. Spatial simulations based on the wave-of-advance model have shown that drift can explain the observed decrease [97]. Other possible explanations include climate [80,96] and cultural [96] effects.

By comparing Neolithic spread rates in several regions of the world, I have proposed some laws [98]. With all of the information available at present (as reviewed above), these laws can be presented and extended (with a sixth law) as follows:

1. First law. The Neolithic spread inland at a rate of about 1 km/yr, but there was substantial variation (0.44-3.6 km/yr). At least the following 13 case studies now support the validity of this law. It is clearly satisfied for the spread of the Neolithic in Europe [8,10,11], across southern Asia [91], in the Balkans [75,76] and three ceramic culture areas, namely the Eastern Linear Pottery [75], the LinearBandKeramik [75] and the Trichterbeckerkultur [75], as well as for the eastern Bantu expansion in Africa [99], the spread of domesticated rice in China and southeastern Asia [100], and the Saladoid-Barrancoid and Incised-Punctuate expansions in tropical South America [92]. In my view, the spread of the Neolithic in Scandinavia [101], the southern Bantu spread [99] and the expansion of Khoi-khoi herders [102] also support this law, because there is no inconsistency with the facts that: (i) the last two case studies also agree with the second law below; and (ii) the Scandinavian one also supports the fifth law below. We stress that the first law does not apply

to modern populations (e.g., the spread of farmers across the United States during the 19th century [103]).

2. Second law. When in addition to demic diffusion there is substantial cultural diffusion, Neolithic spread rates are faster. This law has strong support from mathematical models [50,71,72]. Moreover, it is consistent with the measured rates of two expansions for which cultural diffusion has been proposed to be of importance, namely those of Khoi-khoi herders in southern Africa [102] and the southern Bantu spread in East Africa [99]. For both case studies, the lower bounds (1.2 km/yr and 1.3 km/yr, respectively) are close to 1 km/yr, so they also support the first law.

3. Third law. Neolithic spread rates over the sea take place at about 10 km/yr. Clear examples are the spread of the Neolithic across the western Mediterranean [86] and Austronesia [104].

4. Fourth law. Most inland and coastal Neolithic spreads were mainly demic. The only examples known up to now that might have been mainly cultural was the spread of maize in America [105] and the expansion of Khoi-khoi herders in southern Africa [102]. In fact, in the latter case most of the range for the cultural effect (3%–68%) was below 50%, *i.e.*, mainly demic (Figure 2.5 in ref. [98]). In any case, the fourth law is valid for all 13 case studies of farmers listed in the first law, as well as for the coastal spread of the Neolithic along the western Mediterranean [98].

5. Fifth law. Neolithic spread rates tend to become slower at higher latitudes. This was suggested by a quantitative study on the spread of the Neolithic in Scandinavia and was attributed to small growth rates (which were estimated directly from archaeological data) [101]. This observation is perhaps not surprising, given the fact that in modern human populations reproduction is known to decrease with increasing latitude [106]. The upper bound for Scandinavia (0.84 km/yr) was close to 1 km/yr, which also supports the first law. Another case study that clearly supports the fifth law is the well-known slowdown in northern Europe (see Sec. 2).

6. Sixth law. The Neolithic spreads later and more slowly at higher altitudes above sea level (compared to surrounding regions). A spatial interpolation of early Neolithic dates in Europe has made it possible to map the isochrones every 250 years and this has shown that the Neolithic first surrounded the Alps completely, and only later begun to climb up these mountains (Fig. 1 in ref. [77]). It did so from all directions (Fig. 2 in ref. [77]) and at clearly slower rates (Figs. 1 and 3 in ref. [77]).

The wave-of-advance model has been also applied to expansions of hunter-gatherers, including the post-glacial recolonization of Europe from southern refuges [58], the diffusion of the Clovis culture in North

America [61,107], the early human occupation of southern South America [61,108], the peopling of Australia [148] and the out-of-Africa expansion [60-62] but, as mentioned in Section 1, for hunter-gatherers the paucity of data available at present leads to less precise results than for expansions of farmers.

Numerous mathematical modifications and extensions of Cavalli-Sforza's wave-of-advance model have been reported. Steele reviewed such work and its comparison to the archaeological record [61]. As mentioned in Section 1, a mathematical refinement took into account the number of dimensions (Eq. (3) and Figure 2a). Another refinement took into account the delay time during which newborn humans live with their parents (Eq. (7) and Figure 2b). A third improvement uses, instead of the diffusion coefficient, the complete set of distances Δ_i and probabilities p_i (moved by farmers per generation), besides taking into account mathematically the cohabitation between children and their parents [54,109].

Many mathematical extensions of Cavalli-Sforza's wave-of-advance model take into account several populations, not only those of early farmers. Models with two populations (farmers and hunter-gatherers) are useful for analyzing the effect of interbreeding and/or acculturation on the spread rate [50]. Models with at three populations [73] or more [110] (such as hunter-gatherers, farmers with a given genetic marker, and farmers without it) are necessary to describe genetic clines (see Section 3 below).

Aoki *et al.* [111] proposed a three-population model that was generalized and applied by Patterson *et al.* [112] to the spread of the Neolithic in India. Motivated by ancient DNA results, in a recent paper Aoki [113] has added new terms to the original equations [111], obtaining a set of equations that has solutions with two crucial properties: (i) Neolithic technologies are introduced into Europe by expanding farmers of Anatolian origin rather than hunter-gatherers converted to farming and (ii) hunter-gatherers continue to coexist in Europe with incoming farmers.

Ackland and co-workers developed a three-population model that displays 'cultural boundaries' in which a population trait (language, ceramics, a genetic marker, *etc.*) does not extend because farming is thereafter no longer carried out by the invading population (Neolithics) but by an indigenous one (Mesolithics who have become farmers) [114]. They proposed that this model could account for the western boundary of the linear pottery culture (LBK) in Europe. It is well-known, however, that LBK farmers preferred to settle in loess soils [115,116], which suggests that the location of the LBK boundary was affected by non-homogeneities in the suitability of the land for farming [116]. In the model by Ackland *et al.* the cultural boundary forms even in homogeneous space [87], so its location is not due only

to non-homogeneities such as the presence or absence of loess. According to Figure 2E by Ackland *et al.* [114] farming in *all* of Germany, Denmark, Italy, France and Spain would have been introduced by hunter-gatherers converted into farming and their descendants, which is opposite to the genetic replacement that has been observed using ancient genetic data in all of these regions [47,117–120] (although it is possible that in some specific locations, a substantial portion of hunter-gatherers transformed into farmers).

It has been pointed out [87] that it would be very important to justify the hypothetical interaction terms introduced by Ackland *et al.* [114] in their equations using independent observations or analytical derivations, because those terms are crucial to obtain their conclusions. This also applies to the models by Aoki and co-workers [111,113].

3. Genetic Clines

In 2001, Cavalli-Sforza spent some days in Girona and suggested that genetic clines would be an interesting topic of research. He had published several contributions on clines of individual markers [52,110,121] and had also included very clear discussions about them in his 1984 book with Ammerman [11] (intuitively in pp. 82–84 and using simulations in pp. 126–130). Moreover, he and his co-workers had performed principal component analyses of many genetic markers [29,110], as mentioned above and reviewed by G. Barbujani in a separate paper of this issue [122]. Here we focus only on the analysis of individual clines, a topic that has been sometimes overlooked but is again of interest today [73].

I believe that Cavalli-Sforza would have enjoyed analyzing ancient clines of individual genetic markers. This can be done by means of three steps. (i) to simulate the genetic evolution of Neolithic farmers as they spread and interbred with Mesolithic hunter-gatherers; (ii) to use these simulations to compute the percentage of a genetic marker in farmers as a function of the distance from the Near East (*i.e.*, a genetic cline); and (iii) to compare this simulated cline to observed data. The first two steps were made by Sgaramella-Zonta and Cavalli-Sforza 48 years ago [121]. An example of their results is shown in Figure 4a. This figure shows the simulated cline on a two-dimensional lattice of 11 x 11 square cells (200 x 200 km² each). Farmers disperse from the central cell of the lattice. Without interaction with hunter-gatherers, there is no cline (*i.e.*, the line would be horizontal for $B = 0$). The larger the value of the interaction parameter, B , the larger and more important is the effect and the steeper the cline. Concerning the comparison to observed data (step (iii) above), Cavalli-Sforza and co-workers in year 2000 plotted observed clines of modern DNA separately for Mediterranean and central European populations (Figure 2 in ref. [52]). Unfortunately those observed clines could not be

compared to simulations because population movements and other processes after the Neolithic (with unknown effects) have surely changed the shape of genetic clines, and also because the initial conditions were totally unknown, as explained below. Cavalli-Sforza and I discussed this topic again in Stanford in 2005, but the main problem was still that there were no ancient genetic data to compare to the results of simulations. Still worse, this lack of ancient genetic data implied that the initial conditions (genetic frequencies of hunter-gatherers and Near Eastern farmers), which are necessary to find results from any simulation, were totally unknown at the time.

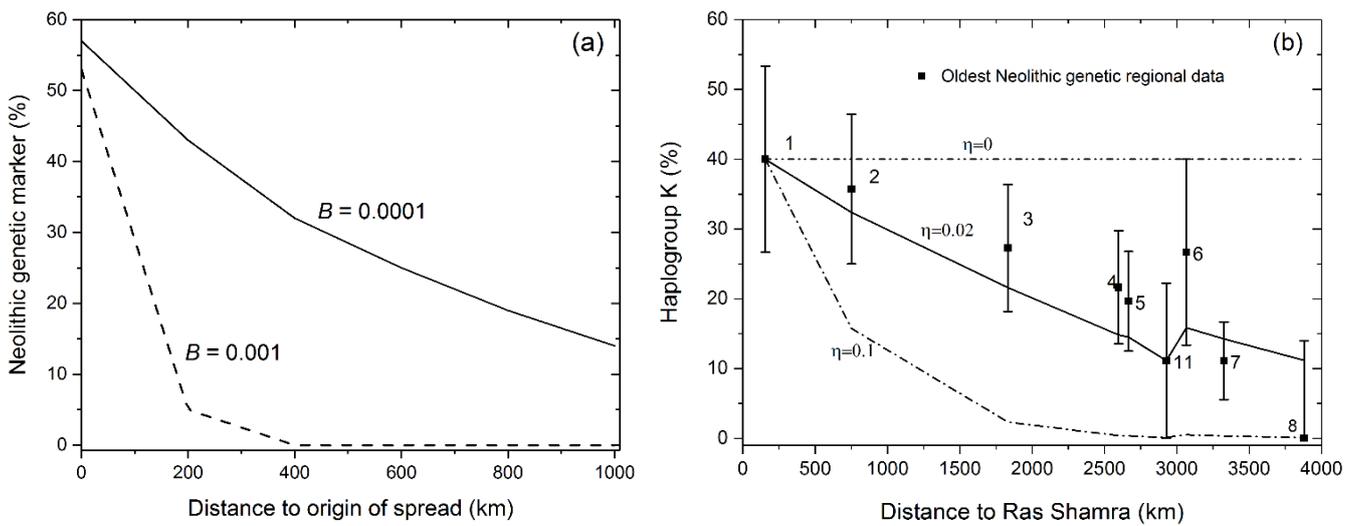


Figure 4 Genetic clines from wave-of-advance models. (a) Genetic cline simulated on a two-dimensional lattice of square cells by Sgaramella-Zonta and Cavalli-Sforza in 1973 [121]. This figure gives the percentage of a genetic marker as a function of position for several values of the Lotka-Volterra interaction parameter, B , between farmers and hunter-gatherers. Initially farmers are at zero distance with a higher density than hunter-gatherers, which are initially elsewhere, and the Neolithic marker has a frequency of 100% at zero distance and 0% elsewhere. The results plotted were obtained at generation 55, so the percentage at zero distance is below 100% (adapted from refs. [11,121]). (b) Genetic cline simulated on a two-dimensional lattice representing a map of Europe. This simulation was performed 44 years after the pioneering one displayed in panel (a). The lines give the simulated percentages of mitochondrial haplogroup K as a function of position from Ras Shamra, the oldest site for region 1 according to the database in Ref. [88]), for several values of the cultural-transmission interaction parameter, η , between farmers and hunter-gatherers (η is the proportion of farmers involved in interbreeding and/or acculturation with hunter-gatherers). The squares and error bars give the corresponding ancient genetic data. The regions are (1) Syria (PPNB culture), (2) Anatolia, (3) Hungary-Croatia (Starcevo culture), (4) eastern Germany (LBK culture), (5) western Germany (LBK), (6) northeastern Spain (Cardial culture), (7) Navarre, (8) coastal Portugal, and (11) Sweden (adapted from ref. [73]).

The paper by Sgaramella-Zonta and Cavalli-Sforza [121] was followed by other simulations of genetic clines. Rendine and co-workers [110] developed numerical simulations on a real map of Europe by assuming several population range expansions (not only the Neolithic one) and a

set of genetic markers with different initial distributions. They used the simulations to compute principal component maps, related the latter to the presumed expansions, and compared these maps to the principal component maps previously obtained from modern genetic data [29]. One of these simulated maps had an extreme in the Near East, and therefore defended that the Neolithic expansion can be identified using principal components [110] (for the reactions of other researchers to this result, see Section 4). They also pointed out [110] that similar pattern had been found from genetic data of modern populations [29].

Barbujani and co-workers obtained genetic clines, again on a real map of Europe, by computer simulation under five different models or scenarios [123]. They showed that the continent-wide clines observed in modern genetic data cannot be explained by the model called 'isolation by distance', a scenario in which there is neither spreading of farmers nor interaction with hunter-gatherers [37,123].

Cavalli-Sforza and his group [124], as well as Currat and co-workers [125,126], modelled the occurrence of mutations and analyzed the phenomenon of 'surfing', rare genetic markers that increase their frequency at the leading edge (pioneering settlements) of a population front (see also ref. [123] and the Editorial of this issue by Chikhi and Barbujani). In ref. [126], two range expansions in Europe were simulated, namely those of modern humans (Paleolithic) and farmers (Neolithic). It was observed that mutations occurring at a front often lead to continent-wide clines for Paleolithic populations, but not for Neolithic ones (due to their higher carrying capacities). This work [126] and the relevance of the surfing phenomenon are further discussed below.

As explained in Section 1, in 2009 ancient genetic data of both early farmers and hunter-gatherers finally became available [47] making it possible to identify which mtDNA haplogroups were present in farmers and absent in hunter-gatherers. In 2017, the data were sufficient to compute percentages of the haplogroups in early farmers with reasonable error bars. They were compared to simulations, and the main results are shown in Figure 4b [73]. It is analogous to Figure 4a, but it includes ancient genetic data (squares and error bars) besides the results of simulations (lines) run on a grid of 180×102 square cells ($50 \times 50 \text{ km}^2$) representing a map of Europe. Figure 4b uses parameter η rather than B (Figure 4a) because Figure 4b is based on cultural transmission theory [50,73], whereas Figure 4a is based on Lotka-Volterra equations [121]. Analogous to Figure 4a, for the model in Figure 4b there is no cline without interaction between farmers and hunter-gatherers (*i.e.*, the line is horizontal for $\eta = 0$). For larger values of the interaction parameter (η in Figure 4b), the cline is steeper (also as in Figure 4a).

In Figure 4b, the minimum frequency in region 11 (Sweden) is observed both in the data and in the simulations. This minimum is due to the existence of two main routes for the spread of the Neolithic in Europe, namely an inland route through the Balkans and central Europe (regions 3–5) and a sea route along the northern Mediterranean coast (regions 6–8). The latter was faster, which implies longer dispersal distances per generation and a less steep genetic cline than along the inland route [73], resulting in the minimum in Figure 4b (both in the data and in the simulations).

In Figure 4b, we see that the simulations agree with all error bars if $\eta = 0.02$. By comparison with simulations using other values of η (not shown in Figure 4b), as well as taking into account the uncertainty in the initial genetic conditions (error bar 1 in Figure 4b), it was estimated that $\eta = 0.01 - 0.03$. According to the definitions of η (Section 2), this means that only between 1% and 3% of farmers were involved in interbreeding and/or acculturation with hunter-gatherers [73]. Therefore, in this sense demic diffusion was much more important than cultural diffusion. It is remarkable that this range (1%–3%) overlaps with a very recent one (2%–6%) obtained using completely different data, methodology and approximations [127]. Indeed, in ref. [127], the whole-genome diversity at several geographic locations was analyzed (rather than the frequency of an individual genetic marker), only the inland route was considered (not the Mediterranean one), and only four locations (along the inland route) were used to compute the effects of migration and interbreeding. Given these substantial differences, the agreement between both ranges seems noteworthy. Previous work on ancient DNA (e.g., ref. [128]) apparently had not estimated the percentage of farmers who interacted with hunter-gatherers. Overall, Figure 4 shows another original idea by Cavalli-Sforza (Figure 4a) that remains clearly influential and useful in present research (Figure 4b).

The topic on genetic clines reviewed in this section is based on genetic data, but it is directly related to the discussion of spread rates in Section 2, which is based on archaeological data. To understand this, let us recall (Section 2) that cultural transmission [70] was combined with demic diffusion in a generalized, demic-cultural model [50] and, by requiring that the spread rate expected from this demic-cultural model agrees with the observed spread rate from archaeological data, it was estimated that the intensity of cultural transmission η was in the range $0 \leq \eta \leq 2.5$ (Figure 3a), which in turn implies that the effect of cultural diffusion on the spread rate had been between 0% and 48% (Figure 3b) [50]. This has been explained in detail in Sec. 2. But using the genetic estimation above, *i.e.*, $0.01 \leq \eta \leq 0.03$ (obtained from the Neolithic cline of haplogroup K in Figure 4b), Figure 3b implies a much narrower estimation, namely that the effect of cultural diffusion on the spread rate was 0.7%–2.3%, *i.e.*, about 1%–2%. This agrees with the

archaeological range above (0%-48%) but is substantially more precise. Therefore, the effect of demic diffusion was 98-99% (see Eqs. (8) and (9)). Admittedly, this is only a first estimation and, in the future, it will be of interest to simulate the clines of additional markers with different shapes and possible explanations. This example shows the potential of combining archaeological and genetic data, as done by Cavalli-Sforza in many of his works.

Besides a combination of cultural diffusion (admixture and/or acculturation) and demic diffusion, could the cline of haplogroup K have other possible explanations? One such explanation is selection, *i.e.*, that some selective pressure *against* haplogroup K caused its frequency to *decrease* (note that the frequency of haplogroup K *diminishes* with increasing distance to the Near East in Figure 4b). However, there are no data indicating the existence of any selective pressure against haplogroup K. Moreover, neutrality tests of Early Neolithic K haplotypes do not show signs of selection (Supp. S1 in ref. [73]). Thus, it would be unreasonable to attribute the existence of this cline (squares and error bars in Figure 4b) to selection. A second possible explanation is isolation by distance, but as mentioned above, continent-wide clines have not been obtained in isolation-by-distance simulations [123]. A third possible explanation is surfing, but in other simulations it was observed that surfing mutations do not lead to continent-wide clines for Neolithic populations [126]. A side issue is that in ref. [126], the spread-rate was found to depend on the carrying capacity of the expanding population, which is at variance with well-established front propagation theory and many other simulations [87]. Clearly these topics and the possible relevance of surfing in Neolithic clines [123–126] deserve further work. It would be of particular interest to determine to what extent the results are affected by using interaction terms derived from cultural transmission theory [50]. In any case, any possible explanation for the cline of haplogroup K (alternative to a combination of demic and cultural diffusion) could be taken seriously only if it could reproduce that cline (squares in Figure 4b) by means of simulations based on realistic assumptions and parameter values.

Cavalli-Sforza and his collaborators also performed wave-of-advance simulations of genetic clines for other purposes. One goal was to infer the place of origin of a population expansion [121]. The limitations of this approach led Cavalli-Sforza to apply the method of principal component maps, as explained on p. 101 of the 1984 book [11]. A second example was to infer the place of origin of a mutation [124]. Other examples were related to the out-of-Africa expansion of modern humans (see the last part of Section 1).

4. Future Progress

During the next few decades, new archaeological data may make it possible to apply the wave-of-advance model to additional Neolithic expansions to those reviewed in Section 2 and refine, confirm or disprove the six laws suggested in Section 2.

Concerning the parametrization of wave-of-advance models, almost all work up to now has followed the early approach by Ammerman and Cavalli-Sforza [11,13] to estimate growth rates from ethnographic data. This is due to the absence of useful archaeological data for performing reliable estimations of population growth. However, in the last decade a new approach has emerged. It is based on the so-called summed probability distributions, which are essentially counts of the number of dated remains as a function of time and space, and are considered a realistic proxy for population numbers. This approach has led to impressive results, such as the discovery of population collapses in many regions of Europe after the initial boom due to the arrival of the Neolithic [129]. Using summed probability distributions, approximate estimations of growth rates were obtained for Scandinavia [101], but more detailed data now make it possible to fit exponential functions. In this way, it is now possible to estimate more realistic growth rates using archaeological rather than ethnographic data [130].

Another issue relevant to the purpose of parametrizing wave-of-advance models is the estimation of dispersal distances Δ_i and probabilities p_i (Sections 1 and 2). In the concluding chapter of their 1984 book, Ammerman and Cavalli-Sforza stressed the importance of this topic as follows: "Much greater challenges are involved in obtaining estimates of migratory activity. At present time, the main source of information along these lines is that provided by ethnography, where data of the kind required are still scarce. It is to be expected that a better understanding of migratory processes in general will emerge as small-scale human populations are studied more closely." Ammerman and Cavalli-Sforza used migratory data from ethnographic fieldwork [11], and all other authors followed the same approach (Section 2); unfortunately, the number of ethnographic studies on migratory activity (values of Δ_i and p_i) is still limited (see Table S2 in ref. [83]). In 2005, it was proposed that genetics could make it possible to estimate the values of Δ_i and p_i for prehistoric populations by identifying ancient parent-child pairs [77]. Such pairs were detected, first with the parent and child buried at the same site [131] and later in different places [132,133]. It seems possible that in coming decades, a sufficient number of such pairs will be detected for Neolithic populations. This could lead to a tremendous increase in the reliability of the parametrization of wave-of-advance models of Neolithic spread.

As additional data become available, the wave-of-advance model will surely be applied to the analysis of genetic clines due to other prehistoric range expansions besides the Neolithic in Europe (Section 3 and Figure 4).

Cavalli-Sforza was interested in all human range expansions, not only in the spread of the Neolithic in Europe. An example is seen in Figure 5, which is a fax with his preliminary calculations on the spread of the Neolithic in Oceania. Also, as explained in Section 1, Cavalli-Sforza was very interested in the spread of cultural traits other than farming. His demic wave-of-advance model has been extended in a model with two dispersal mechanisms, one for individuals and another for cultural traits (non-local cultural transmission) [77]. This makes it possible to apply the wave-of-advance approach even to purely cultural expansions, so future applications may include the spread of innovations, not only in humans but also in other species [134].

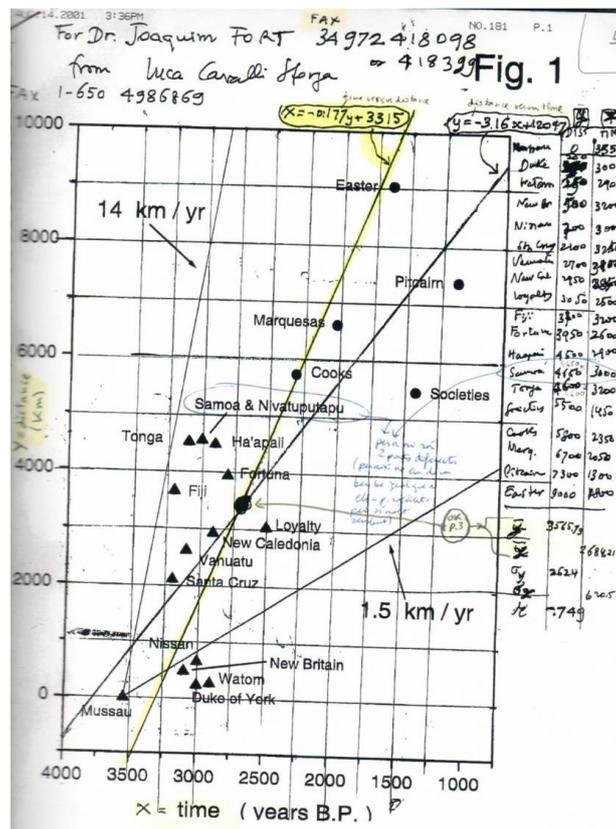


Figure 5 Fax sent by Cavalli-Sforza to the author on August 14th, 2001. It contained preliminary calculations on the spread of the Neolithic in Oceania. Cavalli-Sforza wrote by hand the list of islands, distances and dates on the right, as well as the calculations below them and the equations of two straight lines, which he added to the triangles, circles and two other lines prepared by the author. Later more accurate data were found to analyze this spread, but this figure shows very clearly that Cavalli-Sforza was interested in human range expansions in general, not just in that of the European Neolithic.

5. Looking Back, Looking Forward

Cavalli-Sforza stated clearly that he had the objective to reconstruct human population history using mathematical methods (see ref. [6] and chapter 5 in ref. [2]). In an interview, he explained his reasoning for using mathematics as follows: "I have been always interested in quantitative prediction. I probably should have been a physicist" [135]. An especially appealing feature of the work by Cavalli-Sforza is that, as far as I know, no other researcher has made so many important contributions to mathematical theories of human population history.

None of the work during the last decades that has been reviewed in this paper (Figures 1b, 2b, 3 and 4b) would have been possible without the pioneering contributions by Cavalli-Sforza (Figures 1a, 2a and 4a). These are only a few examples of the many novel ideas introduced by Cavalli-Sforza that were very successful. To the best of my knowledge, no other researcher has made such great discoveries in both science and the humanities. For example, his pioneering work established the major importance of drift in genetics and demic diffusion in archaeology [136]. It is possible that such major discoveries are not always appreciated nowadays. Indeed, a leading researcher on ancient human genetics wrote a few years ago: "The few major new claims that Cavalli-Sforza did make have essentially all been proven wrong" [137]. But this would perhaps not trouble Cavalli-Sforza, because sometimes he had to cope with non-enthusiastic reactions to his work. Some examples are the following. (i) Many archaeologists disagreed with the idea that demic diffusion had driven the spread of the Neolithic in Europe [21–25]. (ii) Alan G. Fix maintained that the main mechanism responsible for genetic clines could have been selection (rather than the combination of demic and cultural diffusion) [138] but in fact selection was not important, see e.g. text S1 in Ref [73]. (iii) Several authors criticized the use of principal component analysis [32,139,140], but Cavalli-Sforza and others defended this method [141–143]. (iv) Robert Sokal originally overstated his contribution to the study of demic diffusion according to Cavalli-Sforza [144], but Sokal eventually kindly acknowledged Cavalli-Sforza's pioneering work in that area [145]. (v) Sykes, Richards and some other geneticists claimed that Cavalli-Sforza had underestimated the genetic contribution of hunter-gatherers [33,35,49] and even suggested that grand syntheses based on the wave-of-advance model should be 'a thing of the past' [35], but their claims were criticized by other geneticists on purely population genetic grounds [36,43,44,146]. Clearly, today Cavalli-Sforza's wave-of-advance model is not 'a thing of the past' at all. It is important in linguistics [66,67,147], archaeology (Section 2) and genetics (Section 3). The wave-of-advance model has been further developed in many directions mathematically and applied to numerous prehistoric spread phenomena. Much more

archaeological and genetic data will become available in the future and the wave-of-advance model will be applied to more case studies, not only concerning spread rates (Section 2) but also to understand ancient genetic clines and their implications (Section 3). Therefore, it is reasonable to expect that the contributions by Cavalli-Sforza reviewed in this paper will remain a gold standard for future work.

Acknowledgements

This work has been partially funded by the Ministerio de Ciencia e Innovación (grant PID2019-104585GB-I00) and the Institució Catalana d'Estudis Avançats (ICREA Academia grant 2022-2026).

Competing Interests

The author has declared that no competing interests exist.

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Cite this article: Fort J. Prehistoric spread rates and genetic clines. *Hum Popul Genet Genom.* 2022;2(2):0003. <https://doi.org/10.47248/hpgg2202020003>