RESEARCH

Cultural versus demic diffusion in agricultural expansions according to three definitions of dispersal distances

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Abstract

Mathematical models of agricultural spread use distances between birthplaces of parents and their children (often called "birthplace distances"). However, the difficulty to find those distances for pre-industrial farmers has often led to the use of other kinds of distances. One example is the distance between the birthplace and the place of residence of each individual ("residence distances"). Another example is the separation between the birthplaces of parents ("mating distances"). It is poorly known to what extent the latter two distances are valid approximations to birthplace distances. In order to address this question, we have prepared a database with the three distances for a specific pre-industrial agricultural population (the Yanomamö). For the spread of the Neolithic in Europe, all three kinds of distances yield spread rates consistent with the archaeological data, as well as cultural effects below 50% (so demic diffusion was more important than cultural diffusion). The three kinds of distances also yield estimations for the percentage of early farmers who interbred with hunter-gatherers that are consistent with the corresponding estimation from genetics. There is wide agreement for the cultural and demic effects in other expansions of agriculture and/or herding (the spread of the Neolithic in Asia, Bantu, and Khoikhoi expansions; the spread of rice in Asia, etc.) and using distances measured for other populations. We conclude that estimates are largely insensitive to the kind of distances used. This implies that the conclusions drawn so far in the literature using these three kinds of distances are robust.

Keywords Agricultural spread · Dispersal kernels · Demic diffusion · Cultural diffusion

Introduction

Ammerman and Cavalli-Sforza (Ammerman et al. 1973; Ammerman and Cavalli-Sforza 1984) were the first to apply a mathematical model (namely, Fisher's wave of advance model) to calculate the spread rate of the Neolithic, i.e., of farming and stockbreeding. This is a purely demic model, i.e., it does not take into account the incorporation of hunter-gatherers into the populations of farmers. In this way, they found reasonable agreement between the calculated spread rate and that implied by the archaeological data. They calculated the spread rate from Fisher's equation, namely

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

where a is the initial growth rate of famers and D is their diffusion coefficient. In order to calculate the spread rate from this equation, they needed the following parameter values. Firstly, the initial growth rate a of farmers can be estimated by fitting an exponential to data of the number of individuals versus time for populations of pre-industrial farmers that settled in empty space. In Sec. S1, we perform such fits for all populations of pre-industrial farmers for which there are detailed ethnographic data (to the best of our knowledge) and find that the overall range is $a = 0.021 - 0.034$ year^{-1} with 95% confidence level (CL). Secondly, the diffusion coefficient in two-dimensional space (the Earth's surface) is given by Fort and Méndez (1999)

$$D = \frac{\sum_{j=1}^{N} p_j r_j^2}{4T}, \tag{2}$$

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where T is the generation time (defined as the average age difference between a parent and his/her children). In Sec. S1, we use all useful ethnographic data available to us for pre-industrial farmers and find the range $T = 28 - 35$ year with 95% CL. Finally, p_j is the probability that an individual (farmers in this case) is born a distance r_j from the birthplace of his father or mother, and N is the number of such distances in the sample of the population considered. The set of probabilities and distances $\{p_j, r_j\}$ is usually called the dispersal kernel. Equations (1)–(2) are used not only in the study of Neolithic spread but also of biological invasions (Ortega-Cejas et al. 2004).

More recently, refined models were developed that take into account a more accurate description of dispersal based on the complete dispersal kernel rather than the diffusion coefficient (2), the cohabitation between parent and their children (which is a special feature of human populations), and the role of cultural in addition to demic diffusion. In this way, the following equation for the spread rate was derived (Fort 2012):

$$s = \min_{\lambda > 0} \frac{aT + \ln\left[(1 + \eta)\left(\sum_{i=1}^{N} p_i I_0(\lambda r_i)\right)\right]}{\lambda T}, \tag{3}$$

where $I_0(\lambda r_i) = \frac{1}{2\pi} \int_0^{2\pi} e^{-\lambda r_i \cos\theta} d\theta$ is the modified Bessel function of the first kind and order zero corresponding to distance r_i in the dispersal kernel. The value of $\lambda > 0$ that minimizes the quotient in Eq. (3) is a measure of the steepness of the population wave of advance (Fort 2012). The angle θ is the dispersal direction, i.e., that of the vector that separates the birthplace of a parent from that of one of his/her children (the previous integral considers all such possible directions, i.e., from 0 to 2π radians = $360°$). Equation (3) is valid under the assumption that dispersal is isotropic (Fort et al. 2007). Finally, η is the cultural transmission intensity. If cultural transmission is due to interbreeding between farmers and hunter-gatherers (vertical cultural transmission (Cavalli-Sforza and Feldman 1981)), η can be interpreted as the portion of pioneering farmers that interbreed with hunter-gatherers and therefore $\eta \leq 1$ (Fort 2011). But if cultural transmission is due to acculturation (horizontal cultural transmission (Cavalli-Sforza and Feldman 1981)), it is possible that $\eta > 1$ because each farmer can convert more than one hunter-gatherer into a farmer (Fort 2012). In general, i.e., under interbreeding and/or acculturation, η can be interpreted as the number of hunter-gatherers that become farmers per pioneering farmer and generation (Fort et al. 2018). In ref. (Isern et al. 2008), it was shown explicitly that for the demic case ($\eta = 0$), Eq. (3) is more accurate than Fisher's Eq. (1). Therefore, in this paper, we shall use Eq. (3). The computer code used is included in the Supp. Info., Sec. S3.

Similarly to the estimations of the values of a and T above, the dispersal kernel $\{p_j, r_j\}$ is estimated from ethnographic data, but Ammerman and Cavalli-Sforza noted that it is more difficult to measure (Ammerman and Cavalli-Sforza 1984). In principle, distances between birthplaces of parent and children should be used but due to the difficulty to find such distances from ethnographic reports on pre-industrial farmers, Ammerman and Cavalli-Sforza used mating distances, defined as distances between the birthplaces of the parents of an individual (see p. 78 in ref. (Ammerman and Cavalli-Sforza 1984)). They also used distances between birthplace and place of current residence (p. 155 in ref. (Ammerman and Cavalli-Sforza 1984)). During the 40 years elapsed since the seminal work by Ammerman and Cavalli-Sforza (Ammerman and Cavalli-Sforza 1984), several authors have used these three kinds of distances (parent–child birthplaces, mating and residence distances) to calculate spread rates of prehistoric farming expansions (Fort and Méndez 1999; Fort et al. 2018; Isern et al. 2008; Cobo et al. 2019; Isern and Fort 2019). These three kinds of distances are also of importance to analyze the genetic structure of populations, for which the most adequate distances are again those between parent and child birthplaces although, as mentioned above, they are also the most difficult to measure (Cavalli-Sforza 1958, 1963; Cavalli-Sforza et al. 1966; Wijsman and Cavalli-Sfroza 1984; Bahuchet et al. 1991; Verdu et al. 2010). The error made when using mating or residence distances has never been estimated because spread rates *for a single population* using these three kinds of distances have never been calculated and compared. The present paper aims to calculate Neolithic spread rates for these three kinds of distances (for a single population) and compare them.

We shall here use the only census available (to the best of our knowledge) that makes it possible to find out these three distances for a single pre-industrial population of farmers. That census (Biella et al. 1997) refers to the Yanomamö, a population in Brazil and Venezuela (Fig. 1) whose subsistence is based on gardening and farming (Chagnon 2013). The census in ref. (Biella et al. 1997) contains the birthplaces and places of residence of individuals, as well as of their parents if known.

Methods

We compute distances (in km) between two locations i and j by using their geographical coordinates (latitudes φ_i and φ_j, and longitudes λ_i and λ_j) into the Haversine equation (Sinnott 1984).

$$d_{ij} = 2R \arcsin\left(\sqrt{\sin^2\left(\frac{\varphi_i - \varphi_j}{2}\right) + \sin^2\left(\frac{\lambda_i - \lambda_j}{2}\right)\cos(\varphi_i)\cos(\varphi_j)}\right), \tag{4}$$
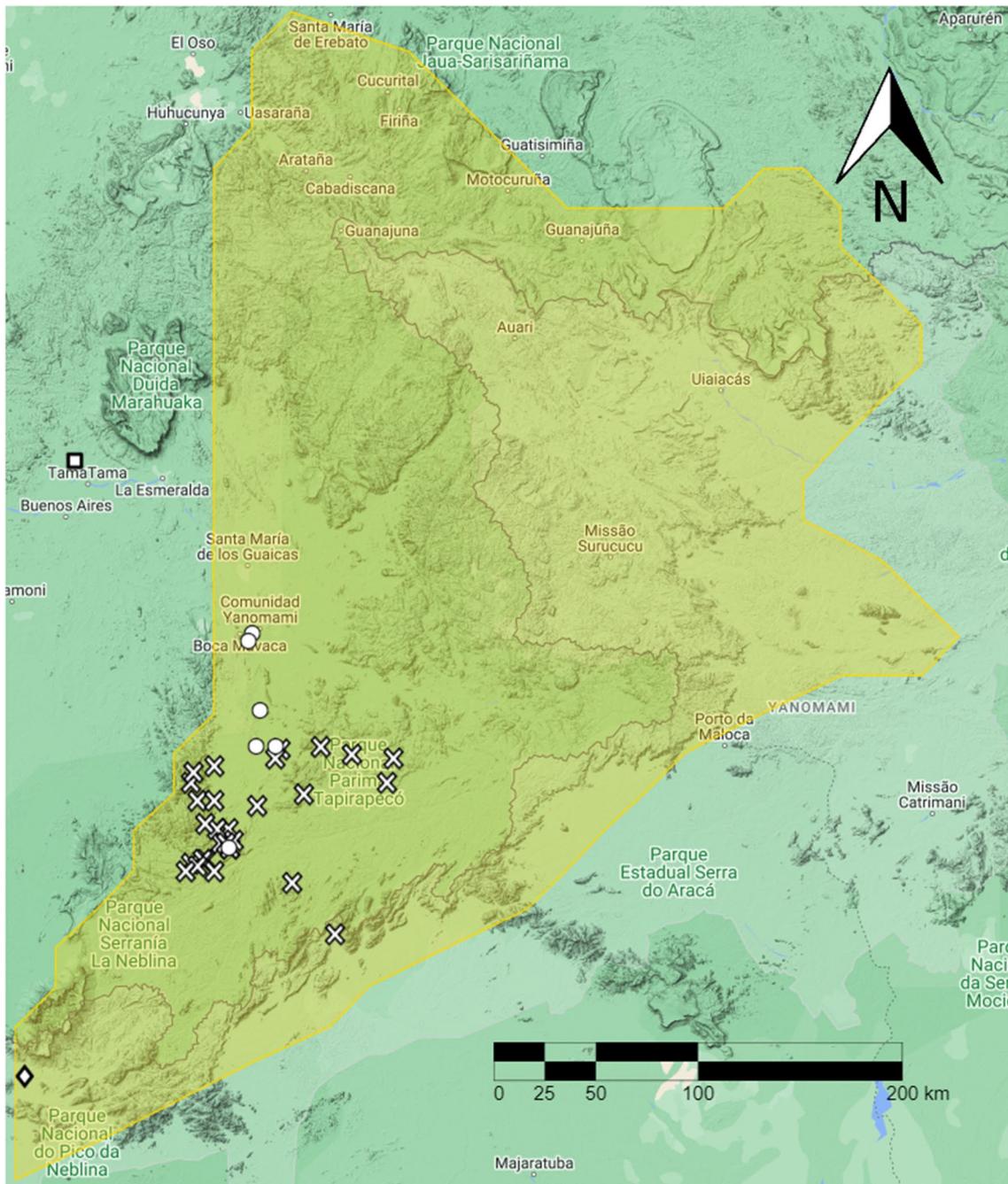
Fig. 1 Map with the locations of birthplaces (crosses) and places of residence (circles) of Yanomamö individuals, obtained from the database of the census in ref. (Biella et al. 1997). The yellow area is the complete region of the Yanomamö population according to ref. (Chagnon 2013). The lower left circle is the only location that is both the birthplace of some individuals and the place of residence of others. There are 80 individuals for which that location is either the birthplace of the place of residence. Additionally, eight individu-als have the same locations of birth and residence (all of them at the lower left circle), and therefore, a distance of residence equal to 0 km (so this circle has the same center as one of the crosses behind it). These 80 + 8 individuals are highlighted in table S2 (kernel R) and explained above it. The rhombus is an anomalous birthplace, and the square is an anomalous place of residence, in the sense that they are very distant from the rest (as discussed in Tables S1-S2)

where R is the average value of the Earth radius ($R = 6371$ km).

Using the census of the pre-industrial agricultural population described above (Biella et al. 1997), we have obtained a database of the three distance types, namely, (i) parent–child birthplace distances (kernel B) for 257 individuals, (ii) distances between birthplace and place of current residence (kernel R) for 159 individuals, and (iii) distances between

birthplaces of father and mother (mating distances, kernel M) for 97 individuals. We include all of the source data and calculated distances in a Supp. Data excel file, separately for birthplace distances (table S1), residence distances (table S2), and mating distances (table S3).

For each kind of distances, we have computed the spread rate as a function of η by using Eq. (3) with all distances available. In other words, the summation in Eq. (3) extends to $N = 257$ for parent–child birthplaces, to $N = 159$ for birthplace-residence distances, and to $N = 97$ for mating distances. For each kind of distances, we have also computed the importance of cultural diffusion by using the following equation (Fort 2012)

$$\% \text{ cultural effect} = \frac{s - s_{\text{demic}}}{s} \cdot 100, \qquad (5)$$

where s is the speed (spread rate) obtained by using Eq. (3), which must agree with the archaeologically observed spread rate. On the other hand, s_{demic} is calculated using Eq. (3) with $\eta = 0$, i.e., s_{demic} is the speed without cultural diffusion (purely demic model). Similarly, the percentage of demic diffusion on the spread rate is defined as (Fort 2022).

$$\% \text{ demic effect} = \frac{s_{\text{demic}}}{s} \cdot 100, \qquad (6)$$

or 100% minus the percentage of cultural effect by Eq. (5).

Parent–child birthplace distances (kernel B)

The first kind of distances are those between the birthplaces of parents and their sons or daughters (kernel B). For our database (Table S1), these birthplaces are represented in Fig. 1 as crosses. The Yanomamö area is shown on yellow background (Chagnon 2013). Each parent–child pair corresponds to two crosses, one for birthplace of the parent and another one for the birthplace of his/her child. From these two locations, we find out the corresponding distance r_j using Eq. (4). All 257 distances obtained in this way are included in Table S1. Since we have 257 parent–child birthplace distances, in Eq. (3), we have used all of these 257 distances, $N = 257$ and $p_i = \frac{1}{257}$.

Figure 2 shows an hypothetical example to explain how the 257 B-distances are applied. In this example, we consider a wave of advance with observed speed or spread rate (estimated from archaeological data) equal to 1.3 km/year (horizontal line in Fig. 2a). By using the 257 B-distances and the values $a = 0.021$ year^{-1} and $T = 35$ year into Eq. (3), we have obtained the dotted curve in Fig. 2a (our computer code is included as Supp. Info., Sec. S3). We note from this curve that for higher values of a (initial growth rate of the farming population), the Neolithic wave of advance propagates more rapidly because there are more farmers. On the other hand,
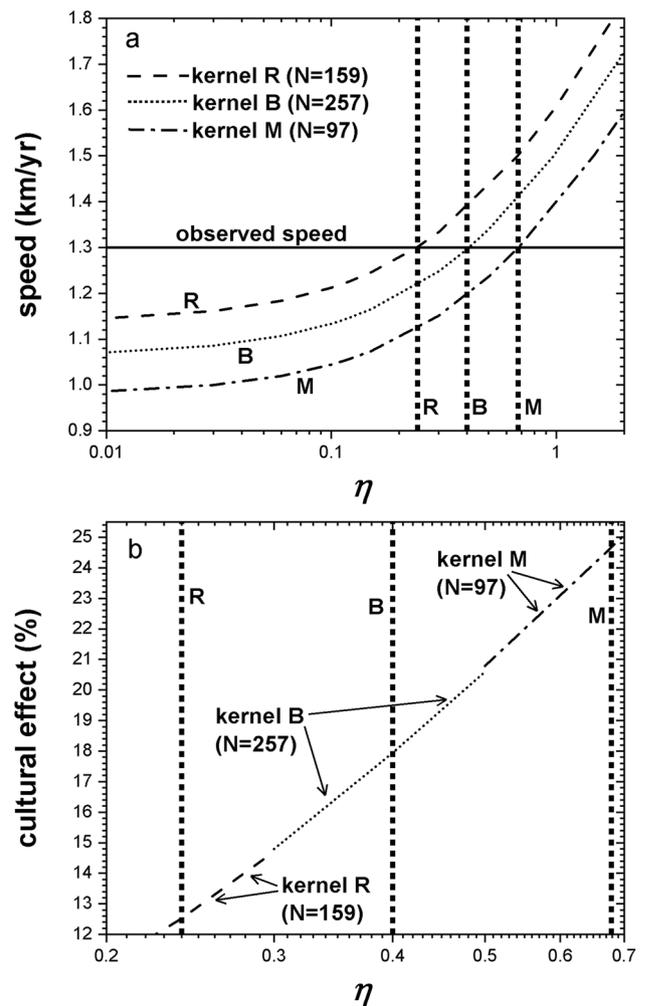

Fig. 2 Hypothetical example. **a** The horizontal line is the observed speed or spread rate (1.3 km/year). The three curves are the calculated speeds from Eq. (3) (i.e., with the code in Sec. S3) using each kind of distances for the Yanomamö (R, B, and M). The value of η in each case is given by the intersection of the horizontal line (observed speed) and the corresponding curve (calculated speed for R, B, or M distances). The values of η are 0.24 (R), 0.40 (B), and 0.68 (M) in this hypothetical example. In all there curves, we have used $a = 0.021$ year^{-1} and $T = 35$ year. **b** Percentage of cultural diffusion computed using Eq. (5). The dashed line in (**b**) has been computed using the dashed line in (**a**). The dotted line in (**b**) has been computed using the dotted line in (**a**). The dashed-dotted line in (**b**) has been computed using the dashed-dotted line in (**a**). The three lines in (**b**) are too close to each other to be distinguished. For this reason, in (**b**), we have plotted only the curve for R distances around the value of η for R distances obtained from (**a**) ($\eta = 0.24$), only the curve for B distances around the value of η for B distances ($\eta = 0.40$), and only the curve for M distances around the value of η for M distances ($\eta = 0.68$)

lower values of T lead to faster speeds because less time elapses between two successive dispersals (generations of farmers). The intersection between the observed speed (horizontal line) and the calculated speed (dotted curve) yields

the value of the intensity of cultural diffusion ($\eta = 0.40$ in this hypothetical example).

In the "Results" section below, we shall generalize this approach by considering real contexts and taking care of the uncertainties in the observed speed as well as in the values of a and T. However, before doing so, we discuss the other two kinds of distances.

Distances between birthplace and place of residence (kernel R)

In this subsection, we consider the distances between the birthplace and place of residence for all individuals for whom the necessary data are available (kernel R). All of them are shown in Fig. 1, where the residence locations are white circles (whereas birthplaces are crosses, as mentioned above). We obtained 159 distances r_j using this method (Table S2), so in Eq. (3), we have used all of these 159 distances, $N = 159$ and $p_i = \frac{1}{159}$. For the same hypothetical example as in the previous paragraph, using these 159 R-distances and the values $a = 0.021$ year^{-1} and $T = 35$ year (as above), we have obtained the dashed curve in Fig. 2a. We observe that the intersection between the observed speed (horizontal line) and the calculated one (dashed curve) implies a different value of cultural diffusion for R distances ($\eta = 0.24$ in this hypothetical example) than for B distances ($\eta = 0.40$, previous subsection).

Distances between birthplaces of spouses (mating distances, kernel M)

The last kind of distances r_j are those between the birthplaces (circles in Fig. 1) of two parents with a common child registered in the database. This kernel has 97 distances for the census analyzed (we stress that this is the only census known to us that has enough data to compute all three kinds of distances for pre-industrial farmers). Since we have 97 mating distances (Table S3), in Eq. (3), we have used all of these 97 distances, $N = 97$ and $p_i = \frac{1}{97}$. For the same hypothetical example as in the previous paragraph, using these 97 M-distances and the values $a = 0.021$ year^{-1} and $T = 35$ year (as above), we have obtained the dashed-dotted curve in Fig. 2a. We observe that the intersection between the observed speed (horizontal line) and the calculated one (dashed-dotted curve) implies, again, a different value of cultural diffusion for M distances ($\eta = 0.68$ in this hypothetical example) than for B or R distances (previous subsections).

The effects of cultural and demic diffusion on the spread rate

In Fig. 2a, we see that the three lines are different, and this is why the precise value of η obtained depends on the kind of distances used (B, R, or M). However, the values of η implied by them (0.40, 0.24, and 0.68, respectively) are rather close to each other if we take into account that all values of η between zero and infinite are possible. Furthermore, Fig. 2b shows that the cultural effect calculated using Eq. (5) and the speeds in Fig. 2a are very similar for the three distances. Indeed, the three curves in Fig. 2b are so close to each other that they cannot be distinguished (in spite of the narrower scale used in Fig. 2b for the horizontal axis). For this reason, in Fig. 2b, we have plotted only the curve for R distances around the value of η for R distances obtained from Fig. 2a ($\eta = 0.24$), only the curve for B distances around the value of η for B distances ($\eta = 0.40$), and only the curve for M distances around the value of η for M distances ($\eta = 0.68$). We think that the reason why the three curves are so similar is that there is an effect of the dispersal kernel on both s and s_{demic} but they are divided in Eqs. (5)–(6) so both effects tend to cancel out to some extent. The important point from Fig. 2b is that the cultural effect (vertical axis) is about 12.5% for R distances, about 18% for B distances, and about 25% for M distances. These values are rather similar, in the sense that all three are clearly below 50%, which implies that cultural diffusion was less important than demic diffusion in this hypothetical example. We conclude that estimates of the cultural effect are largely insensitive to the kind of distances used. This implies that the conclusions drawn so far in the literature using these three kinds of distances are robust. This is the key new finding reported in this paper. Below, we shall check the validity of this conclusion by using data from real archaeological contexts.

Results

The spread of the Neolithic in Europe

Our first real example is the spread of the Neolithic in Europe. The hatched rectangle in Figs. 3a, 4a, and 5a corresponds to the observed range of the spread rate of the Neolithic in Europe (at the continental scale) according to archaeological data, namely $0.9 - 1.3$ km/year (Fort 2012; Pinhasi et al. 2005).

Using B distances, in Fig. 3a, we plot the speed (i.e., spread rate) of the wave of advance obtained from Eq. (3) as two curves. The full curve is the maximum possible speed (obtained using $a = 0.034$ year^{-1} and $T = 28$ year, from the "Introduction" section), and the dashed line is the minimum one (obtained using $a = 0.021$ year^{-1} and $T = 35$ year). Thus, the speeds and values of η according to Eq. (3) are those in the area between the two curves. The intersection of this area and the observed range is shown as a black area. It gives the values of the speed and η that agree both with the archaeological data (hatched rectangle) and with
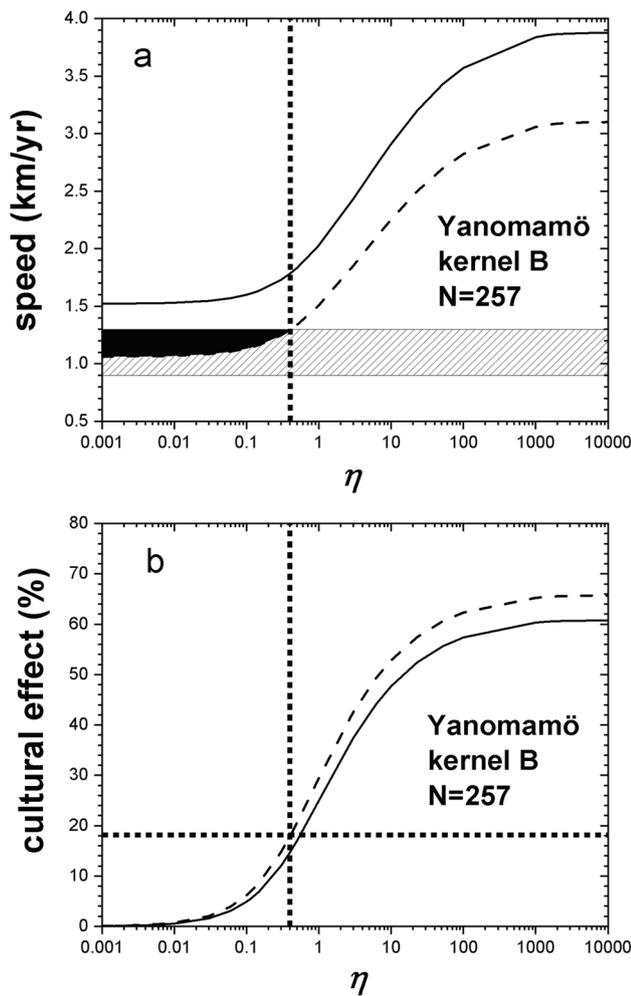
Fig. 3 The spread of the Neolithic in Europe according to B Yanomamö distances. **a** Spread rate as a function of intensity of cultural diffusion η obtained using Eq. (3) (i.e., the code in Sec. S3) and the 257 parent–child birthplace distances included in Table S1 (kernel B). The full line has been obtained for $a = 0.034$ year^{-1} and $T = 28$ year and the dashed one for $a = 0.021$ year^{-1} and $T = 35$ year. The hatched rectangle $(0.9 - 1.3\text{km/year})$ corresponds to the spread rate of the Neolithic in Europe obtained from the archaeological data. **b** The percentage of cultural diffusion computed using Eq. (5). The full line in (**b**) has been computed using the full line in (**a**), and the dashed line in (**b**) has been computed using the dashed line in (**a**)
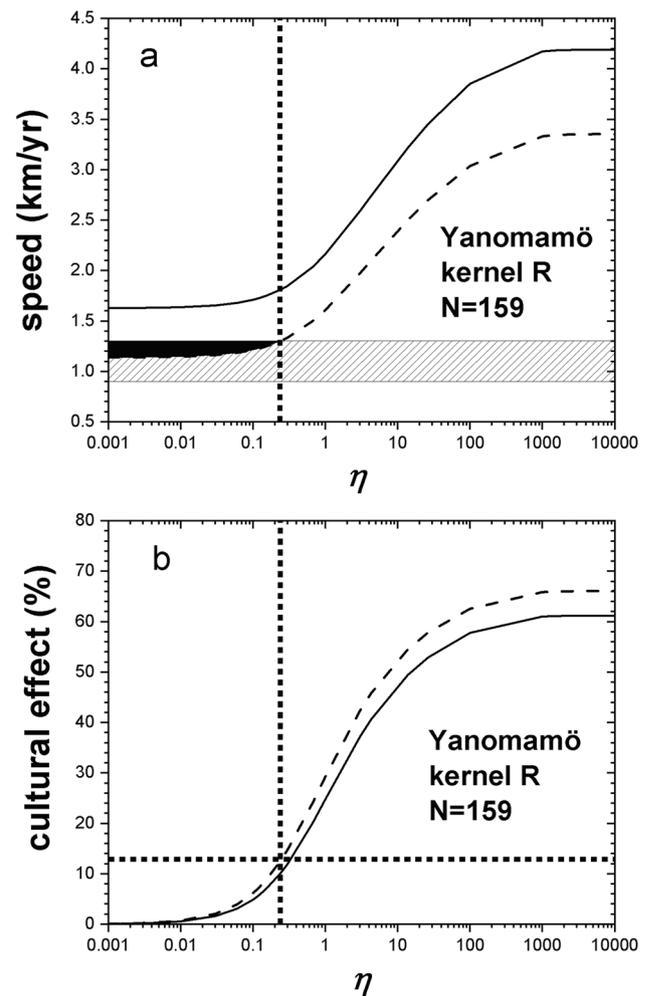
Fig. 4 The spread of the Neolithic in Europe according to R Yanomamö distances. **a** Spread rate as a function of intensity of cultural diffusion η obtained using Eq. (3) (i.e., the code in Sec. S3) and the 159 birthplace-residence distances included in Table S2 (kernel R). The full line has been obtained for $a = 0.034$ year^{-1} and $T = 28$ year and the dashed one for $a = 0.021$ year^{-1} and $T = 35$ year. The hatched rectangle $(0.9 - 1.3\text{km/year})$ corresponds to the spread rate of the Neolithic in Europe obtained from the archaeological data. **b** The percentage of cultural diffusion computed using Eq. (5). The full line in (**b**) has been computed using the full line in (**a**), and the dashed line in (**b**) has been computed using the dashed line in (**a**)

Eq. (3) (area within the two curves). Figure 3a shows that parent–child birthplaces (i.e., B distances) lead to spread rates consistent with the observed one (black area) provided that $\eta < 0.40$. This means that according to kernel B, less than 40% of early farmers interbred with hunter-gatherers during the spread of the Neolithic in Europe. In Fig. 3b, the percentage of cultural effect, calculated using Eq. (5) and the speeds from Fig. 3a, is depicted as a function of η. We can observe that for the allowed range of the cultural transmission intensity ($\eta < 0.40$), the percentage of cultural

diffusion is below 18%, so the percentage of demic diffusion is above 82%. This implies that cultural diffusion was substantially less important than demic diffusion. Next, we enquire how this result changes when using the other two kinds of distances.

Using R distances, Fig. 4a shows the spread speed as a function of η, and Fig. 4b displays the variation of the percentage of cultural diffusion. In this case, we notice that there is consistency between the mathematical model and the archaeological data only if $\eta < 0.24$ (Fig. 4a). Thus,
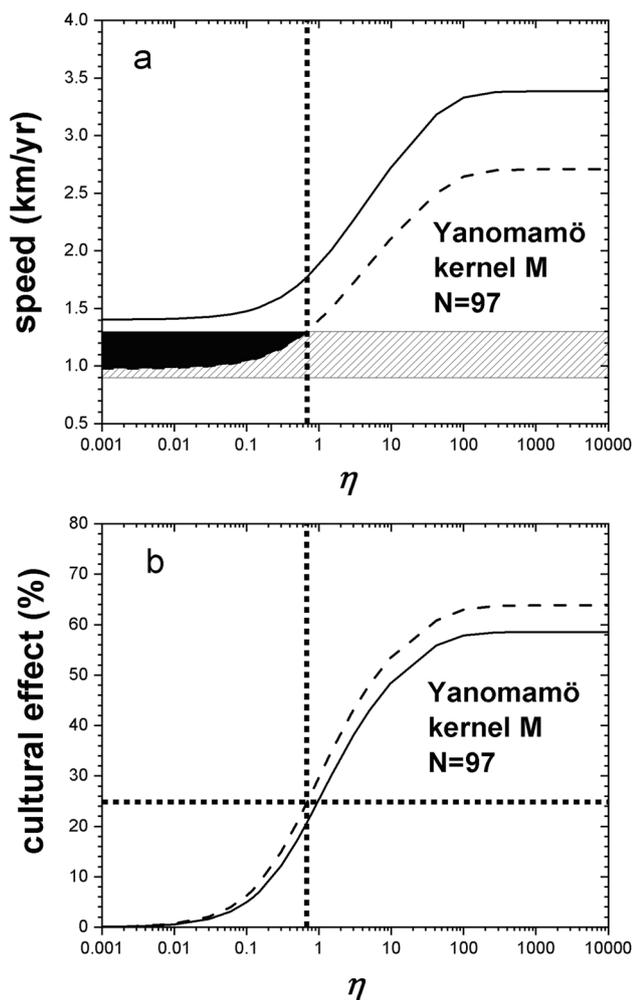
Fig. 5 The spread of the Neolithic in Europe according to M Yanomamö distances. **a** Spread rate as a function of intensity of cultural diffusion η obtained using Eq. (3) (i.e., the code in Sec. S3) and the 97 mating distances included in Table S3 (kernel M). The full line has been obtained for $a = 0.034$ year^{-1} and $T = 28$ year and the dashed one for $a = 0.021$ year^{-1} and $T = 35$ year. The hatched rectangle ($0.9 - 1.3$ km/year) corresponds to the spread rate of the Neolithic in Europe obtained from the archaeological data. **b** The percentage of cultural diffusion computed using Eq. (5). The full line in (**b**) has been computed using the full line in (**a**), and the dashed line in (**b**) has been computed using the dashed line in (**a**)

according to kernel R, less than 24% of early farmers interbred with hunter-gatherers during the spread of the Neolithic in Europe. On the other hand, we see from Fig. 4b that according to kernel R, the cultural effect is lower than 13% so the demic effect is above 87%.

Using M distances, in Fig. 5a, the dependence of the Neolithic spread rate with the cultural diffusion intensity η is represented. We observe that it agrees with the archaeological data for η values lower than 0.68. Thus, according to kernel M, less than 68% of early farmers interbred with hunter-gatherers during the spread of the Neolithic in Europe.

Finally, Fig. 5b shows that the cultural effect is below 25%, and therefore, the demic effect is above 75% according to kernel M.

All three values of the cultural effect are below 50%, which implies that demic diffusion had a more important effect than cultural diffusion on the spread rate of the Neolithic in Europe. Next, we consider other archaeological examples of agricultural waves of advance.

Other contexts of agricultural spread

In order to compare several agricultural expansions, it will be useful to consider additional farming populations (besides the Yanomamö) for which dispersal histograms have been used to model farming expansions. Those histograms are given in Table 1.

Table 2 contains four examples of agricultural expansions with spread rates around 1 km/year, and Table 3 contains four examples of expansions with spread rates above 1 km/ year. We do not consider the very few contexts known with spread rates below 1 km/year because the models proposed to explain them are substantially more complicated mathematically (Fort et al. 2018; Isern and Fort 2010, 2012; Fort 2015). In this way, we can focus our attention on the new point introduced in this paper, i.e., the comparison between B, R, and M distances.

First, we consider agricultural expansions with spread rates about 1 km/year (Table 2). Note from Figs. 3a, 4a, and 5a that the maximum cultural intensity η_{max} is obtained by the intersection of the lower, dashed curve (minimum calculated speed) and the upper side of the hatched rectangle (upper limit of the observed speed). The latter value is 1.3 km/year for the spread of the Neolithic in Europe (Figs. 3a, 4a, and 5a) and also for the spread of the Neolithic in South Asia and the spread of domesticated rice in East Asia (Table 2). This is why for these three case studies (the Neolithic in Europe, the Neolithic in South Asia, and rice in East Asia), for each dispersal kernel (row in Table 2), all results are the same. Thus, in these three contexts, the cultural effect was around 50% or less for all dispersal kernels, i.e., these three agricultural spreads were mainly demic. On the other hand, for the eastern Bantu expansion, the upper limit of the observed speed is not 1.3 km/year but 1.5 km/year, and this leads to higher values of η_{max} and thus of the cultural effect for all dispersal kernels (Table 2). However, also for the eastern Bantu expansion, the cultural effect is below 50% for six of the eight dispersal kernels, and slightly above 50% for the other two (58% for the Issongos and 56% for Markazi). Thus, the results support a mainly demic spread for spread rates of about 1 km/year (Table 2), and this holds for each of the three kinds of distances (B, R, and M).

Several authors have highlighted differences between the archaeological contexts listed in Table 2. Gangal, Sarson,

Table 1 Dispersal histograms of farming populations that have been previously used to analyze agricultural expansions. R stands for residence distances, M for mating distances, and B for parent–child birthplace distances, as defined in "Introduction" and "Methods" sections. For the Yanomamö, histograms of B, R, and M distances are reported in table S4 and plotted in Fig. 6, but they have not been used because we know the complete set of individual distances (tables S1-S3)

Population or area	Probabilities $\{p_1, p_2, p_3, \dots\}$	Distances $\{r_1, r_2, r_3, \dots\}$ (km)
Majangir R (Gilishi 20–29 yr) (Ammerman and Cavalli-Sforza 1984; Isern et al. 2008; Stauder 1971)	{0.40, 0.17, 0.17, 0.26}	{2.4, 14.5, 36.2, 60.4}
Issongos M (Ammerman and Cavalli-Sforza 1984; Isern et al. 2008; Cavalli-Sforza 1971; Cavalli-Sforza and Bodmer 1971)	{0.42, 0.23, 0.16, 0.08, 0.07, 0.02, 0.01, 0.01}	{2.3, 7.3, 15, 25, 35, 45, 55, 100}
Markazi B (Cobo et al. 2019; Mehrai 1984)	0.799, 0.041, 0.022, 0.025, 0.064, 0.004, 0.009, 0.021, 0.015	0.5, 5.5, 15, 25, 35, 50.03, 57.20, 60.51, 97.65
Bihar M (Cobo et al. 2019; Singh and Singh 2015)	0.018, 0.081, 0.105, 0.129, 0.14, 0.125, 0.107, 0.079, 0.068, 0.057, 0.036, 0.025, 0.03	2.5, 7.5, 12.5, 17.5, 22.5, 27.5, 32.5, 37.5, 42.5, 47.5, 52.5, 57.5, 62.5
Chandauli M (Cobo et al. 2019; Shukla 2015)	0.058, 0.122, 0.191, 0.256, 0.168, 0.101, 0.069, 0.023, 0.012	4, 12, 20, 28, 36, 44, 52, 60, 68

Table 2 Some agricultural expansions with spread rates around 1 km/year. The results for the Yanomamö follow from Figs. 3, 4, and 5. The results for the other populations have been found by applying exactly the same method, i.e., by plotting figures analogous to Fig. 3a–b but using the corresponding dispersal histogram for each population in Table 1

Population or area	Context							
	Neolithic Europe (0.9–1.3 km/yr), 7000–4000 BC (Fort 2012; Pinhasi et al. 2005)		Neolithic S. Asia (0.5–1.3 km/yr), 8000–4000 BC (Souza et al. 2022)		Bantu-East (0.5–1.5 km/yr), 1500 BC–500 AD (Isern and Fort 2019)		Rice E. Asia (0.7–1.3 km/yr), 5000 BC–1000 AD (Cobo et al. 2019)	
	η	% cultural	η	% cultural	η	% cultural	η	% cultural
Yanomamö B (Fig. 3)	0–0.40	0–18%	0–0.40	0–18%	0–0.97	0–29%	0–0.40	0–18%
Yanomamö R (Fig. 4)	0–0.24	0–13%	0–0.24	0–13%	0–0.67	0–24%	0–0.24	0–13%
Yanomamö M (Fig. 5)	0–0.68	0–25%	0–0.68	0–25%	0–1.47	0–35%	0–0.68	0–25%
Majangir R (Gilishi 20–29 yr)	0–1.44	0–33%	0–1.44	0–33%	0–3.53	0–42%	0–1.44	0–33%
Issongos M	0–2.79	0–51%	0–2.79	0–51%	0–5.03	0–58%	0–2.79	0–51%
Markazi B	0–2.33	0–49%	0–2.33	0–49%	0–4.19	0–56%	0–2.33	0–49%
Bihar M	0–3.63	0–41%	0–3.63	0–41%	0–10.91	0–49%	0–3.63	0–41%
Chandauli M	0–3.55	0–41%	0–3.55	0–41%	0–10.13	0–48%	0–3.55	0–41%

and Shukurov (Gangal et al. 2014) noted that the spread of the Neolithic from the Near East across South Asia was likely hampered by the arid climate and complicated topography of the Middle East, which make this area less favorable for agriculture than Europe. They also noted that the spread of the Neolithic in Europe was accelerated by sea travel along the northern Mediterranean coastline (Isern et al. 2017a), but, in contrast, the southern coastline of Iran is still more arid than its interior, and this is reflected in a lack of Neolithic sites near the coast (Gangal et al. 2014). On the other hand, the Bantu populations of farmers that expanded in East Africa had already developed iron metallurgy, which makes a major difference with the spread of the Neolithic in Europe and South Asia (Isern and Fort 2019).

Finally, in eastern and southeastern Asia, rice was the main staple cereal that led to the spread of farming (Cobo et al. 2019). In spite of these and other important differences, all four agricultural expansions propagated with essentially the same rate (about 1 km/year) and dominated by demic diffusion (Table 2).

However, some agricultural/herding expansions had spread rates above 1 km/year (Table 3). In these cases, our basic methodology is the same, but its application varies depending on the observed spread rate and the dispersal kernel applied. The simplest case is exemplified by the first context in Table 3 (i.e., the spread of the Neolithic in the Balkans, 1.2–2.1 km/year) and the Yanomamö B kernel (Fig. S8). Then, the shape of the consistency (black) region

Table 3 Some expansions of farming and/or herding with spread rates above 1 km/year. The Khoikhoi was an expansion of herding without farming. See Figs. S8-S10 for some examples of how these results have been obtained

Population or area	Context							
	Balkans Neolithic (1.2–2.1 km/yr), 6000–6250 BC (Porcic et al. 2020)		Bantu-South (1.3–2.5 km/yr), 1500 BC–500 AD (Isern and Fort 2019)		Khoikhoi (1.2–3.6 km/yr), 300 BC–700 AD (Jerardino et al. 2014)		Rice Japan (1.6–2.5 km/yr), 800–200 BC (Crema et al. 2022)	
	η	% cultural	η	% cultural	η	% cultural	η	% cultural
Yanomamö B (Fig. S8)	0–6.23	0–49%	0–22.93	0–57%	0–∞	0–66%	0.1–22.93	5–57%
Yanomamö R	0–4.30	0–46%	0–13.79	0–54%	0–∞	0–66%	0–13.79	0–54%
Yanomamö M	0–9.68	0–53%	0–42.08	0–61%	0–∞	0–64%	0.30–42.08	12–61%
Majangir R (Gilishi 20–29 yr) (Fig. S9)	0–∞	0–49%	0.08–∞	4–49%	0–∞	0–49%	0.87–∞	22–49%
Issongos M (Fig. S10)	0.48–27.79	21–70%	0.74–97.91	27–75%	0.48–∞	21–78%	1.92–97.91	41–75%
Markazi B	0.35–22.55	17–68%	0.58–80.15	24–73%	0.35–∞	17–76%	1.57–80.15	38–73%
Bihar M	0.25–∞	10–57%	0.55–∞	16–57%	0.25–∞	10–57%	2.44–∞	32–57%
Chandauli M	0.23–∞	9–60%	0.53–∞	16–60%	0.23–∞	9–60%	2.39–∞	32–60%

is slightly different (compare Fig. S8 to Fig. 3a), but the value of η_{max} is obtained as before (see the caption to Fig. S8 for details) and yields $\eta_{max} = 6.23$ (as reported in Table 3). Second, more complicated case is exemplified by the same context (the spread of the Neolithic in the Balkans, 1.2–2.1 km/year) but using the Majangir R kernel. For this kernel (Fig. S9), the speeds are slower than for the Yanomamö B kernel (Fig. S8). For this reason, the minimum calculated speed never reaches the upper limit of the observed spread rate, 2.1 km/year (Fig. S9), and this is why $\eta_{max} = \infty$ in Table 3 (see Fig. S9 and its caption for details). Finally, a third case is exemplified again by the same context (the spread of the Neolithic in the Balkans, 1.2–2.1 km/year) but using the Issongos kernel (Fig. S10). In this case, the calculated speeds for $\eta = 0$ are still slower, so slow that they are inconsistent with the observed range, and this leads to a minimum value of $\eta \neq 0$, namely $\eta_{min} = 0.48$ in Table 3 (see Fig. S10 and its caption for details).

The important points from Table 3 are that if the spread rate is sufficiently fast, the value of η_{max} is larger than in slower expansions (Table 2), and furthermore, demic diffusion may not be enough and cultural diffusion can dominate. This is clearly seen for the Bantu-South, Khoikhoi, and Japanese rice expansions (Table 3, last three columns), because the maximum percentage of the cultural effect is above 50% for all eight dispersal kernels except one (and even for this one, it is 49%). However, the minimum percentages of the cultural effect are not above 50% (Table 3), so these results do not imply that these expansions were necessarily mainly cultural. They do suggest that fast expansions (Table 3) could have been either mainly demic or mainly cultural. In other words, they were not necessarily mainly demic, in contrast with the slower expansions summarized in Table 2. This conclusion holds for all three kinds of

distances (B, R, and M) because in all cases, the maximum cultural effect is about 50% or higher for sufficiently fast expansions (Table 3).

Understanding the differences between spread rates using birthplace (B), residence (R), or mating (M) Yanomamö distances

In order to understand the differences between the speeds from the three Yanomamö distances, we have calculated the three corresponding histograms (table S4) and plot them in Fig. 6. We stress that in Figs. 3, 4 and 5, we have not used these histograms but the complete sets of distances, which are more accurate (although they are samples and not the complete population). The histograms in Fig. 6 are useful to understand the tendencies, as follows. We see in Fig. 6 that kernel R (dotted line) displays low probabilities for most of the small distances (lower peak in Fig. 6) and high probabilities for most of the long distances (about 60–90 km). Thus, overall, kernel R implies longer distances moved by farmers (per generation), and this is why it predicts the fastest Neolithic spread rates for all values of η, as can be easily seen by comparing Fig. 4a (kernel R) to Fig. 3a (kernel B) and 5a (kernel M). In the same figures, we see that kernel M is the slowest one, and this is due to the fact that it corresponds, overall, to shorter distances than the other two kernels. Indeed, kernel M tends to attain high probabilities for short distances (peak in Fig. 6, dashed line) and small probabilities for long distances (the dashed line is the lower curve in the range 60–90 km).

In Fig. 7a, we plot the error in the speed due to using kernel R or M instead of the most reliable kernel B. The error in the speed, obtained from Figs. 3a, 4a, and 5a, is between 6 and 9% for kernel R and between 6 and 13% for
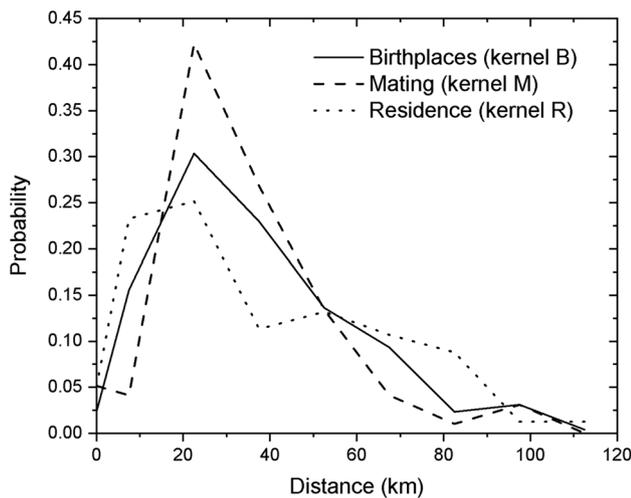
Fig. 6 Histograms of distances calculated from the three Yanomamö lists of distances used in this paper (table S4), namely parent-children birthplaces (kernel B), birthplace-residence distances (kernel R), and distances between birthplaces of spouses (mating distances, kernel M). There is a first bin corresponding to a null distance. For each of the other bins, we have used its average distance (i.e., 7.5 km, 22.5 km, …, 112.5 km). All probabilities and distances are given in Table S4

kernel M (Fig. 7a). These errors are rather small if we take into account that, in contrast, there is a substantial error in the observed speed from the data (0.9–1.3 km/year implies an error of about 18% relative to the mean). We conclude that according to the census data analyzed, it is reasonable to use any of the three kinds of distances. This suggests that the results from previous work, e.g., refs. (Ammerman and Cavalli-Sforza 1984; Fort and Méndez 1999; Fort et al. 2018; Isern et al. 2008) and many others, are reliable. The main point of the present work is that spread rates from these three kinds of distances *for a single population* have been here compared for the first time, so we have been able to estimate the error due to distance kernels R and M relative to the most appropriate one, namely kernel B. We emphasize that kernel B is the most precise one because it is used in the mathematical model leading to Eq. (3). However, for kernel B, there are very few ethnographic data available for pre-industrial farmers, as noted previously (Ammerman and Cavalli-Sforza 1984; Isern et al. 2008; Cavalli-Sforza 1963; Wijsman and Cavalli-Sfroza 1984). Therefore, it is reassuring that kernels R and M also yield reliable spread rates and estimations of the effects of cultural and demic diffusion.

We note that the speeds from kernel R (Fig. 4a) are slightly above those from the most reliable kernel B (Fig. 3a). In contrast, the speeds from kernel M (Fig. 5a) are slightly below those from the most reliable kernel B (Fig. 3a). Thus, the speeds from kernel B are bounded by those of kernels R and M for the Yanomamö. Unfortunately, we cannot test this in other populations because we
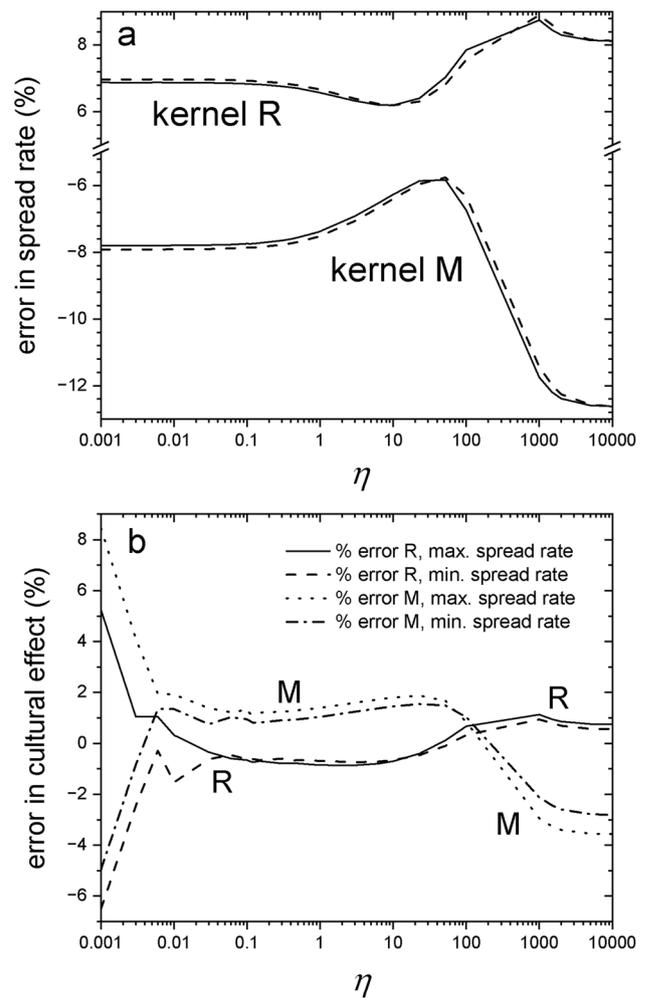

Fig. 7 **a** Error in the spread rate of the Neolithic in Europe, due to using kernel R or M instead of kernel B. The full line (maximum spread rate) has been obtained for $a = 0.034$ year^{-1} and $T = 28$ year and the dashed line (minimum spread rate) for $a = 0.021$ year^{-1} and $T = 35$ year. **b** Error in the cultural effect of the Neolithic in Europe, due to using kernel R or M instead of kernel B. The curves for the maximum spread rates have been obtained for $a = 0.034$ year^{-1} and $T = 28$ year and the curves for the minimum spread rates for $a = 0.021$ year^{-1} and $T = 35$ year

would need all three kernels and they are not available (as far as we know). However, it is interesting that the differences between the speeds from kernels R and B are < 9%, and the differences between the speeds from kernels M and B are < 13% (Fig. 7a). Thus, the errors of kernels R and M are small and similar in magnitude. This suggests that considering other populations (different from the Yanomamö) for which kernel B is unknown will presumably yield a similar error, regardless of which kernel (R or M) is available. Moreover, the error will be likely small compared to that of the spread rate, as estimated from archaeological data (which is about 18% for the European Neolithic, as explained above).

From Figs. 3b, 4b, and 5b, we note that the cultural effect (percentage of speed due to cultural diffusion) is very similar for all three kernels. This is important because it suggests that the relative percentage of demic and cultural diffusion can be estimated by using distances of any of the three kinds (B, R, and M). In order to quantify this point, using the results from Figs. 3b, 4b, and 5b, we have calculated the error in the cultural effect due to using kernel R or M instead of the most reliable kernel B (Fig. 7b). We see that the cultural effect for kernel R differs by < 7% from that of kernel B (Fig. 7b). Similarly, the cultural effect for kernel M differs by < 9% from that for kernel B (Fig. 7b). Thus, also for the cultural effect, using dispersal distances R or M for other populations (different from the Yanomamö) will presumably yield a small error compared to kernel B. We stress that we compare to kernel B because it is the most precise one due to the fact that it is used in the mathematical model leading to Eq. (3).

The question of what percentage of early farmers interbred with hunter-gatherers is of considerable interest. We have seen that for the spread of the Neolithic in Europe, kernel B (Fig. 3a) implies this percentage in the range 0–40%, kernel R (Fig. 4a) suggests 0–24%, and kernel M (Fig. 5a) indicates 0–68%. Again, the result from the most reliable kernel B (namely, a maximum of 40%) is bracketed by those of kernels R and M (24% and 68%, respectively). The fact that kernel B yields a result intermediate between those of kernels R and M suggests that using kernels R or M (for populations such that kernel B is unknown) may be a reasonable approach to estimate the maximum percentage of early farmers who interbred with hunter-gatherers. If both distances R and M are available, an interval can be also obtained (for Neolithic Europe, we have seen that this interval is 24–68% compared to the more precise value of 40% from kernel B). For prehistoric farming expansions different from Neolithic Europe, the maximum proportion of farmers that interbred with hunter-gatherers (value of η) estimated using Yanomamö B-distances is always intermediate between the values using Yanomamö R and M distances (Tables 2 and 3).

Other ethnographic populations

Mathematical models of Neolithic spread use distances between the birthplaces of parent and children (B distances) (Fort and Pujol 2008). It has been suggested that in the future, it may be possible to measure B distances for prehistoric populations by means of the genetic identification of parent–child pairs buried in different places (Fort et al. 2018; Fort 2015, 2020, 2021). However, there are not enough such data at present. This is why we have to use ethnographic data from extant populations instead. The main aim of this paper is to compare three kinds of such distances (B, R, and M)

and their implications in modelling agricultural spread in prehistory. It is more reasonable to use distances from pre-industrial populations than from industrialized ones. The reason is that many of the latter experienced a sharp increase in mobility with the introduction of mechanized forms of transport (Boyce et al. 1971; Mehrai 1984). We have used distances for the Yanomamö, a population of horticultural-ists inhabiting the Amazonian rainforest. The Yanomamö are a pre-industrial population, in fact the only one for which the three kind of distances (B, R, and M) are available (to the best of our knowledge). But a limitation of using their distances is that we cannot know if they are similar or not to those of the prehistoric populations that lived in the contexts that we wish to model (e.g., early Neolithic Europe). It is reasonable to expect that intergenerational distances may be conditioned by factors such as post-marital residence rules, settlement density, environment, etc. The quantitative importance of such potential effects is unknown due to the paucity of data available. Nevertheless, it is possible to compare intergenerational distances (and their implications) for several ethnographic populations. As mentioned above, in Table 1, we have gathered distance histograms for five farming populations (different from the Yanomamö) that have been previously used to model prehistoric agricultural spread. The Majangir (Ethiopia) and the Issongos (Central African Republic) are pre-industrial farmers, and their dispersal kernels have been used in studies on the spread of the Neolithic in Europe (Ammerman and Cavalli-Sforza 1984; Fort 2012) and Bantu expansions (Isern and Fort 2019). Markazi (Iran), Bihar (India), and Chandauli (India) are rural populations whose dispersal kernels have been used to model some expansions of farmers (Cobo et al. 2019) and herders (Jerardino et al. 2014). Table 1 includes B, R, and M distances but unfortunately, only one of these three kinds of distances is known for each of these five populations. We observe that they are broadly comparable to those of the Yanomamö (Fig. 6), in the sense that the maximum distance is about 100 km or less for all populations (in fact this is a crucial difference with some industrialized populations (Fort and Pareta 2020)). This is of interest because, as mentioned above, there are various reasons for individuals to change their residence, and they will have an effect on dispersal distances. One such reason is marriage, but not the only one. Some Yanomamö villages come into existence as larger villages fission into smaller ones, grow, fission again, and occupy new lands (p. 33 in Chagnon (2013)). A third reason for the Yanomamö to move is the abduction of women by men from other villages (chapter 6 in Chagnon (2013)). Similarly, the Majangir were often raided for slaves to trade or for women and children to be incorporated into the raiding groups (Stauder 1972). A fourth reason is the breaking of social rules, e.g., by incestuous marriage in the Yanomämo (p. 155 in Chagnon (2013)). A fifth one is separation of some

individuals to avoid extreme violence after conflict, which in turn may have many possible origins. Within the Majangir, these include broken marriages, re-marriages, suspicions of adultery, sexual jealousy, arguments over bridewealth, accusations of thefts of honey, etc. (Stauder 1972). A sixth reason is that sometimes, warfare or raids drive out most of the people from specific areas (p. 77 in Chagnon (2013)). A seventh reason is the desire of young people to improve their economic and social situation by moving elsewhere, as observed in some ethnographic populations (Hofmann 2016). Surely subsistence and environmental factors can also have an effect in specific cases. Given the existence of so many influences, it is remarkable that the distances in Fig. 6 and Table 1 are not so different after all.

Although the number of populations for which intergenerational distances are known (Table 1) is clearly too low to reach any conclusions on universal differences between B, R, and M distances, we can make the following interesting observations.

Firstly, according to the first column in Table 2 (Neolithic Europe) using any of the three Yanomamö distances (B, R, and M), the maximum value η_{max} of the intensity of cultural diffusion is always $\eta_{max} < 1$. However, this result is of no general validity because it does not hold for the populations in Table 1. Indeed, they all lead to values $\eta_{max} > 1$, more precisely between 1.44 and 3.63 (Table 2, column Neolithic Europe). But interbreeding cannot lead to values of $\eta > 1$, as explained in the paragraph below Eq. (3) (Fort 2011). Therefore, interbreeding might not have been enough, and acculturation (e.g., the conversion of complete families of hunter-gatherers into farmers) might perhaps have taken place in case the histograms of those populations (Table 1) were closer to the real ones in early Neolithic Europe. However, even in the hypothetical case that the histograms of the populations in Table 1 were more realistic than those of the Yanomamö, it would be also possible than only interbreeding took place. The reason is that for all populations in Table 1, $\eta < 1$ is also possible since the minimum value η_{min} of the intensity of cultural diffusion is $\eta_{min} = 0$ in all cases (Table 2, column Neolithic Europe). This is due to the fact that the consistency range between the observed and the calculated spread rates include $\eta = 0$ for all populations (e.g., in Figs. 3a, 4a, and 5a, the black region extends to the left-hand side of the plots).

Secondly, all eight dispersal kernels are consistent with a purely demic spread, i.e., a percentage of cultural diffusion of 0% (Table 2, column Neolithic Europe). The Issongos and Markazi populations lead to the higher maximum cultural effects, 52% and 49%, respectively. The reason is that for these two populations, demic diffusion has less importance because the percentage of dispersal distances longer than 35 km is less than 12%, whereas for all other six histograms, it is more than 29% (Table 1 and Fig. 6 or table S4). The maximum cultural effect is less than 50% for all populations except for the Issongos, whose dispersal distances are bounded because they live in a very limited region and rarely mate with nearby populations (p. 78 in ref. (Ammerman and Cavalli-Sforza 1984)). This exemplifies the fact that intergenerational distances can be affected by many factors, as discussed above. But even for the Issongos, the maximum percentage of cultural diffusion for the spread of the Neolithic in Europe (51%) is very close to 50%, and for all other seven histograms (rows in Table 1), it is below 50%. Thus, in spite of the fact that the Yanomamö (Fig. 6) and the other populations (Table 1) display different dispersal kernels, these results strongly suggest that the spread of the Neolithic in Europe was mainly demic. This agrees qualitatively with the genetic turnover that took place with the arrival of the Neolithic in most of Europe (Bramanti et al. 2009). Usually, this turnover is quantified by estimating percentages of ancestry of early Neolithic genomes (Mathieson, et al. 2015). However, those percentages of ancestry cannot be used to calculate the percentages of the demic and cultural diffusion on the spread rate (as done in the present paper using archaeological data), because no mathematical relationship between them is known. For the purposes of the present paper, it is important to emphasize that all three kinds of distances (B, R, and M) agree in the conclusion that the spread of the Neolithic in Europe was mainly demic (Table 2, column Neolithic Europe). Similarly, for the other archaeological contexts in Tables 2 and 3, the three kinds of distances widely agree concerning the dominance of demic or cultural diffusion.

Conclusions

We have mainly considered the Yanomamö population because it has, as far as we know, the only census available for pre-industrial farmers with the data necessary to estimate three different kinds of distances, namely those of parent–child birthplaces (kernel B), birthplace-residence places (kernel R), and birthplaces of parents (mating distances, kernel M). These three kernels agree in the sense that they all imply a spread rate that is consistent with that estimated from archaeological data for the spread of the Neolithic in Europe (black regions in Figs. 3a, 4a, and 5a). They also agree in that demic diffusion was more important than cultural diffusion in the spread of the Neolithic in Europe, in the sense that for all three kernels, the effect of cultural diffusion on the spread rate is below 50% (18% from Fig. 3b, 13% from Fig. 4b, and 25% from Fig. 5b). In our opinion, the fact that the maximum cultural effect is similar (between 18 and 25%) for all three kernels (for the same population) suggests that any of the three kernels leads to acceptable results to estimate the relative importance of demic and cultural

diffusion. The same conclusion holds for other prehistoric dispersals of farming and/or herding (Tables 2 and 3).

We stress that kernel B is the most appropriate one because it is used in the mathematical reproduction-dispersal-interbreeding model leading to Eq. (3). However, there are very few ethnographic data for kernel B (Fort 2020). As mentioned above, kernels R and M yield spread rates similar to those from kernel B, and this confirms the validity of previous work using kernels R and/or M, e.g., in refs. (Ammerman and Cavalli-Sforza 1984; Fort and Méndez 1999; Fort et al. 2018; Isern et al. 2008).

The percentage of early farmers who interbred with hunter-gatherers is an important quantity, although it is difficult to estimate from archaeological data. For the spread of the Neolithic in Europe, kernel B implies for this percentage the range 0–40% (i.e., $0 \leq \eta \leq 0.40$, from Fig. 3a), kernel R implies the range 0–24% ($0 \leq \eta \leq 0.24$, from Fig. 4a), and kernel M implies the range 0–68% ($0 \leq \eta \leq 0.68$, from Fig. 5a). The uncertainty of these results is due to the slow variation of the spread rate with the intensity of interbreeding η for low values of the latter (left part of the curves in Figs. 3a, 4a, and 5a), which in turns leads to a wide consistency region with the spread rate estimated from archaeological data (black region in the same figures). However, it is worth to note that all three results are consistent with the only genetic estimation so far obtained for this percentage in this case study (the spread of the Neolithic in Europe), namely 1–3% (Isern et al. 2017b).

Both the distances and the spread rates of kernel B are between those of kernels R and M for the Yanomamö. This suggests that kernels R or M can be used to provide useful estimations (or even intervals) for the spread rate, the percentage of farmers that interbred with hunter-gatherers, and the percentage of cultural diffusion (specially if data for kernel B are inaccurate or unavailable).

For the Yanomamö, we can compare the three kernels and have found that kernel R has the longest distances moved per generation (Fig. 6) and consequently leads to the fastest spread rates, whereas kernel M has the shortest distances and therefore yields the slowest spread rates. However, the errors in the spread rate for kernels R and M (relative to kernel B) are small, below 9% and 13%, respectively (Fig. 7a). These errors seem quite acceptable, specially if we take into account that the spread rate of the Neolithic in Europe (as estimated from the archaeological data) has a rather larger error (about 18%).

Using dispersal kernels of other populations (different from the Yanomamö) and considering other agricultural/herding expansions (different from the Neolithic in Europe), the three kinds of distances (M, R, and M) strongly suggest that expansions with speeds of about 1 km/year are mainly demic (Table 2). They also indicate that expansions with spread rates faster than 1 km/year may be either mainly demic or mainly cultural (Table 3).

In such fast expansions (Table 3), the intensity of cultural transmission η can attain higher values than in slower expansions (Table 2).

In some expansions with speeds of about 1 km/year (e.g., the spread of the Neolithic in Europe and South Asia and the spread of rice in East Asia), the three Yanomamö kernels suggest that interbreeding could have been the main mechanism of cultural transmission ($\eta < 1$), but the kernels of other populations are also consistent with the possibility of an important role for acculturation ($\eta > 1$). However, for such slow expansions (Table 2), all distance kernels are also consistent with purely demic diffusion ($\eta = 0$).

It is worth to keep in mind that there are several sources of uncertainty. Firstly, the range for the spread rate of the Neolithic in Europe that we have used (0.9–1.3 km/year) had been previously estimated by linear regression over the whole continent (Fort 2012; Pinhasi et al. 2005). This method leads to a statistically sound value for the spread rate (the correlation coefficient is very high, $R = 0.83$) (Fort 2012; Pinhasi et al. 2005) and a bracket for its error (the range above has 95% CL), but this estimate is only an average rate that neglects regional variations (Fort 2015). Secondly, taking into account the calibrated probability distribution for each date would increase the precision of the linear fit and thus of the spread rate. Thirdly, it is reasonable to expect that in future work, additional radiocarbon dates and further filtering of the existing databases (specially to take care of the old wood effect) will lead to more precise estimations (both at the continental and at the regional levels). Concerning the model parameters, we believe that Sec. S1 contains the most detailed and statistically sound estimation (with 95% CL) of the uncertainties in the initial growth rate a and the generation time T. For the dispersal kernel, Tables 2 and 3 quantify the uncertainties, although we stress that this paper shows that B, R, and M distances lead to similar results by comparing for the first time the results using these distances for a single population (the Yanomamö). Using dispersal kernels for other populations, the effect of this uncertainty shows up clearly (Tables 2 and 3), although there is wide overall agreement as far as the dominance of demic and cultural diffusion is concerned. Finally, there is some uncertainty due to the mathematical model itself, specially because it is based on isotropic dispersal. This assumption cannot be tested archaeologically at present but if this becomes possible in the future, perhaps it will be possible to find realistic parameter ranges for more detailed, non-isotropic models (Fort 2020).

Declarations

Competing interests The authors declare no competing interests.

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