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Long-distance dispersal effects and Neolithic waves of advance

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ABSTRACT

Mathematical models of Neolithic spread use dispersal histograms to estimate some of the parameters necessary to obtain quantitative spread rates that can be compared to those inferred from the archaeological record. However, it has been never determined if dispersal histograms are a reasonable approximation to the complete distribution of dispersal distances. Indeed, it is unknown if long-distance dispersal events are important in Neolithic spread, similarly to what happens in many ecological invasions. In this paper, we first exemplify the possible importance of long-distance dispersal by using a detailed histogram for a modern, industrialized population. We show that using such an histogram yields substantially faster spread rates than those of Neolithic waves of advance, and that this is due to the existence of long-distance dispersal events (of several hundred kilometers). Next we address the question of whether such a behavior is also observed in pre-industrial populations. For this purpose, we use a complete set of dispersal distances for the individuals of a pre-industrial population for the first time, and we find that long-distance dispersal events (i.e., of several hundred kilometers) are absent. We also show that, using this complete set of dispersal distances, the spread rates predicted by a mathematical model are consistent with those of the Neolithic, both in continental Europe and in Scandinavia. Moreover we observe, quite surprisingly, that computing histograms (even with only 4 bins) from the complete set of individual distances introduces negligible changes in the results. We argue that these results (the absence of long-distance dispersal events, the agreement with the archaeological record, and the validity of the histogram approach) imply that the propagation of Neolithic waves of advance can be described using a sound mathematical approach, which also yields reliable estimates on the relative importance of demic and cultural diffusion. This is applied to several case studies (Europe, Scandinavia and some specific ceramic cultures in Neolithic Europe).

1. Introduction

It has been proposed that farming and herding could have spread geographically in prehistory via two different mechanisms (or a combination of them), namely demic and cultural diffusion. Ammerman and Cavalli-Sforza defined demic diffusion as the case in which farming spreads due to the dispersal and reproduction of farmers (i.e., Neolithic populations) (Ammerman and Cavalli-Sforza, 1971). Cultural diffusion, on the other hand, corresponds to the case in which farming spreads because indigenous hunter-gatherers learn agriculture from Neolithic farmers (Ammerman and Cavalli-Sforza, 1971). The mathematical analysis of prehistoric spread rates was initially performed using models that included only demic diffusion (Ammerman and Cavalli-Sforza, 1971, 1984; Ammerman and Cavalli-Sforza, 1973; Fort and Méndez, 1999; Fort et al., 2004a; Pinhasi et al., 2005). More recently a mathematical model was developed that includes cultural in addition to demic diffusion (Fort, 2012). In this framework, the spread of a human wave of advance can be driven by a combination of demic and cultural diffusion. The model in Ref. (Fort, 2012) makes it possible to estimate the relative importance of cultural and demic diffusion (using the spread rate inferred from archaeological data) and has been recently applied to case studies of Neolithic spread in several continents (Fort, 2012; Jerardino et al., 2014; Isern et al., 2017a; Fort et al., 2018; Isern and Fort, 2019; Cobo et al., 2019).

In order to compute a Neolithic spread rate (in kilometers per year) using a mathematical model, it is necessary to know several parameter values, among them the probability that an individual moves as a function of the distance that she/he moves (during the time interval from, e.g., her/his birth until that of one of her/his children). This probability as a function of distance is called the dispersal kernel (Clark,

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1998). Up to now, all studies on Neolithic spread rates (including those summarized in the previous paragraph) have used, as estimations of the dispersal kernel, histograms published in ethnographic reports of modern industrialized and/or pre-industrial farmers. Each such histogram is a list of dispersal probabilities, each one corresponding to a distance interval (the latter is also called a bin). It has been never analyzed whether histograms are a reasonable approximation to the real distribution of distances or not, for the purpose of estimating the spread rate and the percentages of demic and cultural diffusion. Clearly, it is necessary to clarify this issue in order to establish whether the histograms used so far, when combined with mathematical Neolithic spread models, can be trusted or not. This is the problem that we will tackle in the present paper.

Our interest in the validity of histograms is motivated by findings in Ecology suggesting that histograms often have an outstanding limitation, due to the fact that they include the longest dispersal distances in an upper-distance bin for which usually only a minimum distance is reported. For example, the longest-distance bin in the histograms in Figs. 5.8-B and C in Ref. (Ammerman and Cavalli-Sforza, 1984) is labelled as '>100 km'. Note that this upper-distance class surely includes longer (and possibly substantially longer) distances than its minimum one (100 km in this example). But it is well-known from Ecology that the longest distances in a dispersal histogram can have a very important effect on the spread rate of a biological invasion (as predicted by mathematical models) (Clark, 1998). In other words, long distances (even if rare) can lead to substantially faster spread rates (this effect is called long-distance dispersal in Ecology) (Clark, 1998; Fort, 2007). For our purposes it is worth to note that in Neolithic waves of advance, such a change in the spread rate (predicted by the mathematical model) will also modify the estimated percentages of demic and cultural diffusion (this follows directly from the theory in Ref. (Fort, 2012)). Therefore, it is necessary to examine carefully the influence of long-distance dispersal in order to determine to what extent using histograms yields valid Neolithic spread rates (and estimates of the relative importance of demic and cultural diffusion).

In order to examine whether histograms are a useful description of dispersal or not, we begin in Sec. 2.1 by considering one of the very few histograms that are detailed enough to include distances of several hundred kilometers. This histogram was recorded for a modern industrialized population (not a pre-industrial one), but is useful to grasp the importance of long-distance dispersal in human populations. We shall find that long distances have a dramatic effect on the spread rate, making it substantially faster than the spread of the Neolithic in Europe. This implies that dispersal data from modern industrialized populations cannot be always applied to Neolithic dispersal, and that it is necessary to determine if pre-industrial populations also display such long distances or not. Such an analysis has not been done before and will be attempted in Sec. 2.2. If pre-industrial populations do display so long distances as industrialized populations (i.e., several hundred kilometers), then the predicted spread rates will be too fast to agree with the archaeological record, and this contradiction will be due presumably to the fact that prehistoric populations did not display so long dispersal distances as modern pre-industrial ones. On the contrary, if modern pre-industrial populations do not display so long distances as modern industrialized populations, then modern pre-industrial populations may have similar dispersal kernels to those of prehistoric populations, and it will make sense to use their dispersal data to simulate the spread of the Neolithic. Note that unfortunately archaeological data cannot be used to determine precise intergenerational dispersal distances for prehistoric populations, although it has been proposed that this might be possible in the future using genetic approaches (Fort, 2015).

In Sec. 2.2 we consider a pre-industrial population and determine if individuals move so long distances as the industrialized population in Sec. 2.1 (i.e., several hundred kilometers) or not. Note that histograms reported in the literature are not useful for this (because they include the longest distances in a single class labelled, e.g., '>100 km'). Fortunately, however, we have found a very interesting dataset for a pre-industrial farmers that makes it possible, for the first time, to determine the distance moved by each individual in the population. Furthermore, we will be also able to construct histograms and compare their results to those using the complete set of individual distances. This analysis will make it possible to determine under which conditions histograms provide trustable values of the Neolithic spread rate and the relative importance of cultural and demic diffusion.

Finally, we will apply this approach to several case studies of Neolithic spread: Europe (Sec. 3), Scandinavia (Sec. 4) and some specific ceramic cultures in Neolithic Europe (Sec. 5).

2. Long-distance dispersal in human populations

2.1. An industrialized population

Early models of Neolithic spread used dispersal histograms of rural modern populations in industrialized countries (see, e.g., Fig. 5.8-A in Ref. (Ammerman and Cavalli-Sforza, 1984)) because dispersal data for pre-industrial farmers are much more difficult to find.

In this section we consider, as an illustrative example of long-distance dispersal effects on spread rates, one of the very few published histograms that are detailed enough to include distances above 100 km (as mentioned in the introduction, most histograms are not so detailed because usually all such distances are grouped into a singles class and labelled, e.g., '>100 km' (Ammerman and Cavalli-Sforza, 1984; MacDonald and Hewlett, 1999)).

Boyce et al. computed an histogram with distances up to 604 km from census data of villages in the Otmoor area (Oxfordshire, England) in 1861 (Boyce et al., 1971) (see also Refs. (Küchemann et al., 1967; Boyce et al., 1967)). The histogram of this rural population is shown in Fig. 1. We note that, whereas most movements have distances below about 100 km, a few portion (5%) have longer distances. As mentioned in the previous section, ecological theory (Clark, 1998; Fort, 2007) has shown that even if long distances have small probabilities, they can substantially increase the speed of population fronts (Neolithic waves of advance in our case). Therefore, we ask if the inclusion of long displacements (above about 100 km in Fig. 1) has a noticeable effect on the

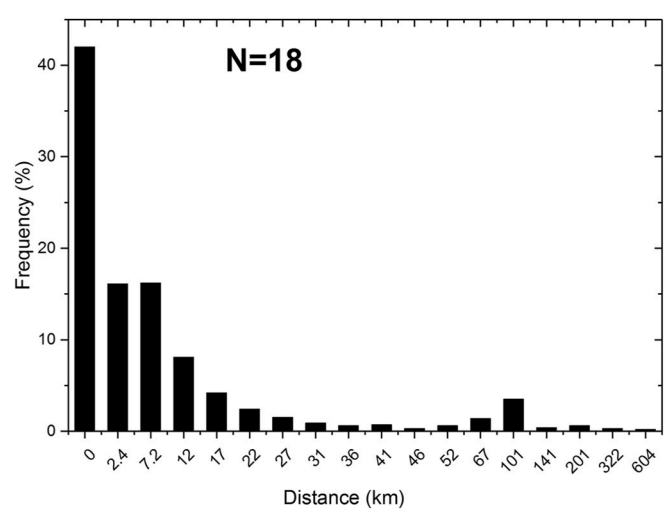

Fig. 1. Histogram of distances moved by individuals in villages in the Otmoor area (Oxfordshire, England) in 1861, as estimated using marriage distances by Boyce et al. (adapted from Fig. 2 in Ref. (Boyce et al., 1971), see also Refs. (Küchemann et al., 1967; Boyce et al., 1967)). The 18 frequencies or probabilities are (from left to right) 0.420, 0.161, 0.162, 0.081, 0.042, 0.024, 0.015, 0.009, 0.006, 0.007, 0.003, 0.006, 0.014, 0.035, 0.004, 0.006, 0.003 and 0.002. The sum of the last five probabilities is 0.05 or 5%, and they correspond to movements with distances longer than 100 km.

front speed or not. To answer this question, we will first compute spread rates using the complete histogram in Fig. 1 (i.e., with all $N = 18$ distance classes in Fig. 1, up to 604 km), and later we will compare the results with the spread rates obtained by neglecting long-distance displacements.

The speed or spread rate of a Neolithic wave of advance is computed using the following equation, which was derived in Ref. (Fort, 2012),

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

where a and T are the net reproduction rate and the generation time of farmers, respectively. Cultural diffusion is included by means of parameter C, which is called the intensity of cultural diffusion and is equal to the number of hunter-gatherers that adopt agriculture per pioneering farmer and generation (Fort, 2012). It does not seem possible to perform direct, reliable estimations of C from ethnographic or archaeological data (and Genetics has been applied to this problem only in one instance so far (Isern et al., 2017b)), so we will plot the spread rate as a function of C. Demic diffusion is included in Eq. (1) by means of the summation in the last parentheses, which takes into account the

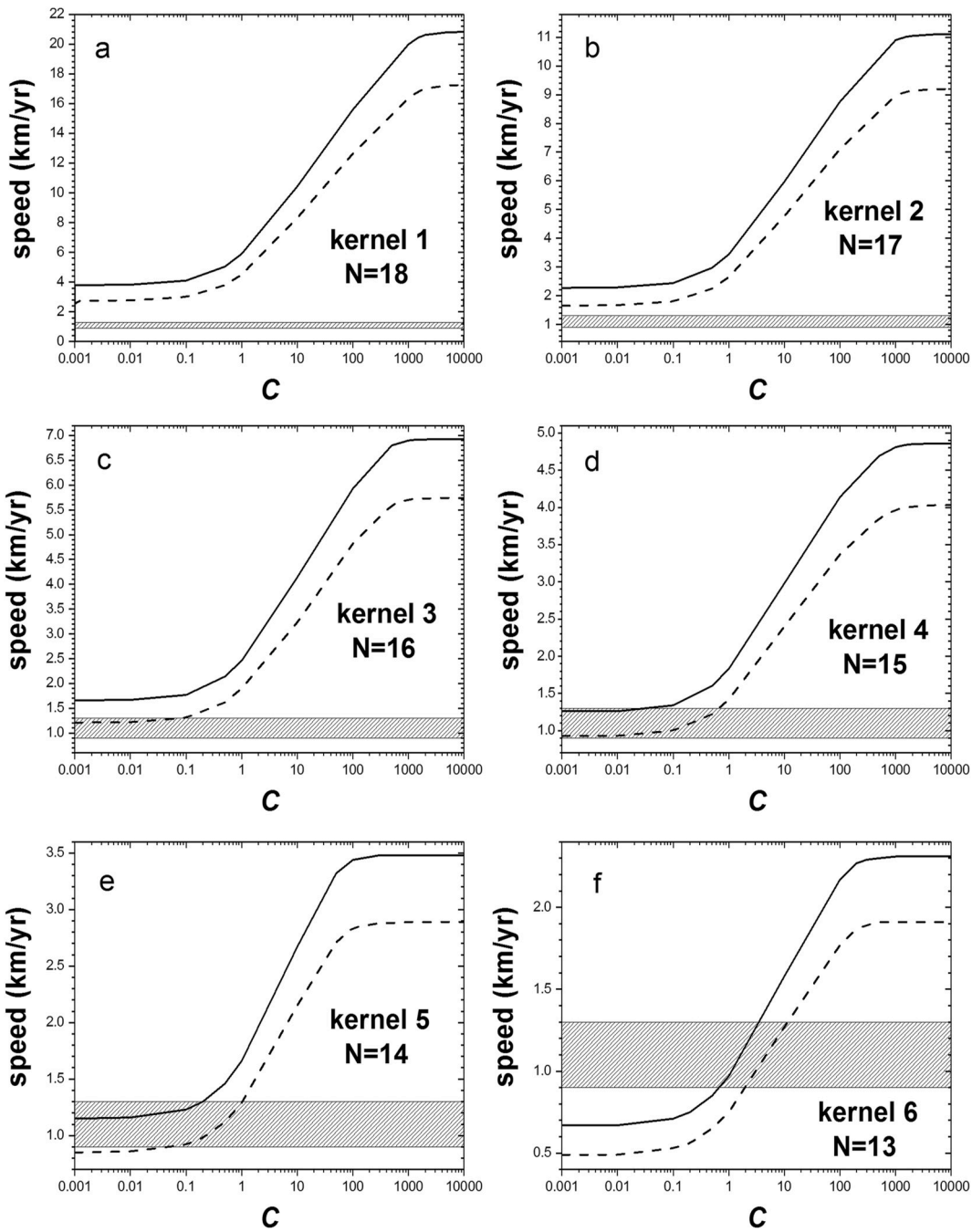

Fig. 2. Panel (a) gives spread rates according to Eq. (1) and the complete histogram in Fig. 1 (N = 18 bins), i.e., distances up to 604 km. Plots (b–f) neglect long-distance dispersal (defined as the bins corresponding to the longest distances in Fig. 1) by including only the first N = 17, 16, 15, 14 and 13 bins, respectively, i.e., distances up to 322 km, 201 km, 141 km, 101 km and 67 km, respectively (see Fig. 1). Full curves have been obtained from Eq. (1) using the highest growth rate ($a = 0.033\ \mathrm{yr}^{-1}$) and the smallest generation time ($T = 29$ yr). Dashed curves have been obtained from Eq. (1) using the lowest reproduction rate ($a = 0.023\ \mathrm{yr}^{-1}$) and the largest generation time ($T = 35$ yr). In all panels, the hatched rectangle gives the observed spread rate of the Neolithic in Europe (more precisely, in the Near East, Anatolia, continental Europe and Great Britain), i.e., 0.9–1.3 km/yr.

probability p_i that an individual of the farmer population disperses a distance r_i (for N possible distances). The values of p_i and r_i are given by the dispersal histogram (for example, for Fig. 1 we have $p_1 = 0.420$, $r_1 = 0$km; $p_2 = 0.161$, $r_2 = 2.4$km; etc.). The function $I_0(\lambda r_i) = \frac{1}{2\pi}\int_0^{2\pi} exp[-\lambda r_i cos\theta]d\theta$ is the modified Bessel function of the first kind and order zero, and λ is a positive parameter. The front speed s is found by plotting the quotient in Eq. (1) as a function of λ for given values of a, T, C, p_i and r_i ($i = 1, 2, \ldots, N$). The speed s is that of the minimum in this plot (Fort, 2012). The net reproduction rate (also called initial growth rate) a has been estimated, from ethnographic data of pre-industrial farming populations settling in empty space, to be in the range $0.023\text{yr}^{-1} \leq a \leq 0.033\ \text{yr}^{-1}$ (Isern et al., 2008). The generation time T is defined as the mean age difference between a parent and one of his/her children (not necessarily the oldest one) (Fort et al., 2004b), and has been estimated to be in the range $29 \leq T \leq 35$ yr for preindustrial farmers (Pinhasi et al., 2005; Fort et al., 2004b). The highest growth rate ($a = 0.033\ \text{yr}^{-1}$) and the smallest generation time ($T = 29$ yr) yield the fastest spread rate for the parameter ranges considered (Fort, 2012) (full curves in Fig. 2). Similarly, the lowest reproduction rate ($a = 0.023\ \text{yr}^{-1}$) and largest generation time ($T = 35$ yr) yield the slowest spread rate (Fort, 2012) (dashed curves in Fig. 2).

Fig. 2a shows the spread rates obtained from Eq. (1) using the values of p_i and r_i ($i = 1, 2, \ldots, N$) from the complete histogram in Fig. 1 ($N = 18$). For each curve, the spread rate increases with increasing values of C because this corresponds to more hunter-gatherers becoming farmers per generation and, obviously, a larger population of farmers spreads farming faster. The maximum (asymptotic) values of the curves in Fig. 2a can be also understood intuitively, as follows. If many new farmers appear every generation ($C \to \infty$), the spread rate will attain is maximum possible value, which is obviously the longest distance in the histogram divided by the generation time (i.e., the interval between two successive displacements). This is why the maximum value of the full curve in Fig. 2a is 604 km/29 yr = 20.8 km/yr, and the maximum value of the dashed curve in Fig. 2a is 604 km/35 yr = 17.3 km/yr.

In Fig. 2b–f we plot the spread rates obtained by excluding long-distance movements, as follows. In Fig. 2b we exclude only the longest distance class (604 km), so we consider $N = 17$ distance classes, divide all 17 frequencies by their sum (so that they add up to one), and compute the spread rates using Eq. (1) with this new histogram (which has distances up to 322 km, see Fig. 1). The same procedure is repeated by neglecting the two longest distance classes (Fig. 2c, $N = 16$, distances up to 201 km), the three longest ones (Fig. 2d, $N = 15$, distances up to 141 km), the four longest ones (Fig. 2e, $N = 14$, distances up to 101 km), and finally the five longest ones (Fig. 2f, $N = 13$, distances up to 67 km).

For comparison, all plots in Fig. 2 include a horizontal hatched rectangle which corresponds to the range 0.9-1.3 km/yr, as implied by archaeological data for the spread rate of the Neolithic in Europe (more precisely, this rate is an average over the Near East, Anatolia, continental Europe and Great Britain) (Pinhasi et al., 2005; Fort, 2012). In Fig. 2a the spread rate predicted by the model (area between the two curves) is faster than the observed speed (hatched rectangle). This indicates that the histogram in Fig. 1 has too long distances to be realistic for Neolithic farmers. Therefore, long-distance dispersal is indeed important in models of human range expansions. This is confirmed by the rest of the panels in Fig. 2, as we next explain. The predicted spread rates (area between the two curves) in Fig. 2b are slower than in Fig. 2a, as expected because the curves in Fig. 2b have been computed by excluding the longest distance in Fig. 1 (604 km), but the predicted spread rates in Fig. 2b are still too fast to agree with the observed spread rate of the Neolithic in Europe (hatched rectangle). As expected, the predicted spread rates become slower if additional long-distance movements are excluded (Fig. 2c–f). Moreover, in Fig. 2c (which neglects the two longest distances in Fig. 1, i.e., 604 km and 322 km) the area between the two curves (predicted speeds) intersects the hatched rectangle (observed speed range). This does not happen in Fig. 2a and b, and it indicates that the displacements of Neolithic farmers were shorter than about 200 km per generation (because the longest distance included in Fig. 2c is 201 km). Similarly, the predicted spread rates become even slower in Fig. 2d and e (which correspond to a maximum distance of 141 km and 101 km, respectively), but are still consistent with the observed rate even in the absence of cultural diffusion ($C = 0$). In contrast, in Fig. 2f (maximum distance of 67 km), consistency between theory and observations is achieved only under the assumption that cultural transmission was sufficiently strong, namely $C \geq 1$, which would imply that at least one hunter-gatherer would have been converted into farmer per each pioneering farmer and generation. Although this point is not central to the present paper, for completeness we mention that such a high value of C seems unlikely for the spread of the Neolithic in Europe, according to an estimation of C based on analyzing a Neolithic mitochondrial cline in Europe (Isern et al., 2017b). For our purposes, the important conclusion from Fig. 2 is that populations with long-distance dispersal (such as that with the histogram shown in Fig. 1) cannot yield spread rates consistent with the archaeological dates of early Neolithic sites in Europe. This strongly suggests that the dispersal behavior of early Neolithic populations in Europe did not include long-distance movements (defined as those longer than about 200 km). Therefore, it is very important to determine if pre-industrial populations (whose histograms are used in Neolithic spread models) display such long distances or not. If they do, they cannot be useful to parametrize Neolithic spread models. We tackle this question in the next subsection.

2.2. A pre-industrial population

Previous work on Neolithic spread models has not taken into account the possibility of long-distance dispersal because, as explained in the introduction, distances have never been reported individually. Instead, long ones are always grouped under a singles class labelled, e.g., '>100 km' (Ammerman and Cavalli-Sforza, 1984), so the histogram does not make it possible to know the percentage (or probability) of movements with distances within each long-distance range (e.g., 100–150 km, 150–200 km, etc.). Fortunately, in this paper we will be able to overcome this limitation thanks to the fact that Biella et al. (1997) published a detailed population census that is, in fact, the only one available for a pre-industrial population (to the best of our knowledge). That population belongs to the Yanomamö, a tribe of tropical forest Indians who live in a remote corner of Amazonia, on the border between Venezuela and Brazil. They are mainly agriculturalists, and their practices include gardening, slash-and-burn farming, hunting and gathering. The census by Biella et al. (1997) is based on the data for the village of Mishimishimaböwei-teri in 1971, as reported by Napoleon A. Chagnon, who collected meticulous demographic and dispersal data during his periods of residence with the Yanomamö (his fieldwork begun when he spent 15 months living with them between 1964 and 1966, and made many additional stays later, spending a total of 41 months in their villages) (Biella et al., 1997; Chagnon, 2013). We think that this population was genuinely pre-industrial at the time of data collection, because it was then described as follows (Chagnon, 2013): (i) The Yanomamö had lived until very recently in isolation, up to the point that the authorities in Venezuela and Brazil knew very little about their existence; (ii) Due to their isolation, they had retained their native social patterns without any interference from the outside world (obviously, they spoke only their own language and had no writing); and (iii) Some of their villages were still uncontacted (Chagnon, 2013).

The census by Biella et al. (1997) includes, among other information, the place of birth and the parents of each individual. In this census, which was published in CD-ROM format (Biella et al., 1997), we located 160 parent-child pairs for which it was possible to determine the distance between the birthplaces of each parent and his/her child (for this purpose, we also used the latitudes and longitudes of the locations reported in the 'gardens and villages' file included in the same CD-ROM as

the census file (Biella et al., 1997)). We include the complete information for the 160 parent-child pairs as Supp. Info. Table S1, where the maximum dispersal distance per generation is 101.1 km. Interestingly, this distance is substantially shorter than the maximum value for the industrialized population in Fig. 1 (604 km). This suggests that perhaps using the dispersal data of this pre-industrial population could yield agreement with Neolithic spread rates (whereas the industrialized population in Fig. 1 does not, as we have seen in Fig. 2a). In order to check this possibility, we will compute spread rates using the individual data of all 160 pairs of individuals, i.e. Eq. (1) with $N = 160$.

It will be also of interest to see how the results change if we use, instead of all 160 distances, an histogram (i.e., a few set of distance classes), as done in all Neolithic spread models up to now (e.g., Ammerman and Cavalli-Sforza, 1984; Isern et al., 2008; Fort, 2012; Fort et al., 2018). For this reason, we have distributed the 160 distances (Table S1) in several classes and computed an histogram with $N = 11$ bins or distance classes (Fig. 3a). For comparison, we have also computed an histogram with only $N = 4$ distance classes (Fig. 3b). This last case ($N = 4$) is rather relevant, because Neolithic spread models have often used histograms with only $N = 4$ distance classes (e.g., p. 139 in Ref. (Stauder, 1971), p. 155 in Ref. (Ammerman and Cavalli-Sforza, 1984), and kernels A-C in Ref. (Isern et al., 2008)). Therefore, it is important to determine if an histogram with $N = 4$ bins (Fig. 3b) yields trustable results or not. These three kernels, which provide alternative descriptions of a single population and have $N = 160$ distances (Table S1), $N = 11$ distances or bins (Fig. 3a) and $N = 4$ distances or bins (Fig. 3b), will be applied to the spread of the Neolithic in Europe (more precisely, in the Near East, Anatolia, continental Europe and Great Britain) on one hand (Sec. 3), and in Scandinavia on the other (Sec. 4). An isochrone map of both case studies is shown in Fig. 4, which shows that the second spread (Scandinavia) was substantially slower than the former (Europe). Finally, we shall also analyze the spread of several specific Neolithic cultures in Europe (Sec. 5).

In Fig. 5a we apply the complete set of raw distances ($N = 160$) to Eq. (1), with the same ranges of a and T as in the previous subsection. We can see that using the exact kernel (complete set of 160 distances) yields agreement (black area in Fig. 5a) with the spread rate of the Neolithic in Europe (more precisely, with an average rate estimated over the Near East, Anatolia, continental Europe and Great Britain) according to the archaeological data (hatched rectangle in Fig. 5a or 0.9–1.3 km/yr, i.e., the same range as in Fig. 2). This shows the validity of the suggestion above, i.e. that the dispersal distances of the pre-industrial population are sufficiently short (as compared to those of the industrialized population in Fig. 1) to yield agreement between the mathematical spread model and the archaeological record.

If we use the histograms with $N = 11$or $N = 4$ (both of them obtained from the complete set of 160 distances), we obtain Figs. 6a and 7a, respectively. Interestingly, similarly to Fig. 5a, in both Figs. 6a and 7a there is agreement between the model and the archaeological data (black region). More importantly, Figs. 5a, 6a and 7a are very similar to each other. Therefore, using histograms, both with $N = 11$bins (Fig. 6a) and with $N = 4$ bins (Fig. 7a), leads to much the same results as using the complete set of 160 distances (Fig. 5a). This establishes, for the first time, the validity of using histograms in Neolithic spread range models.

It is worth to mention that Eq. (1) is based on a minimal model (Fort, 2012), in the sense that it has few parameters and this makes it possible to use independent data to estimate them (and therefore, to obtain results without choosing neither fitting any parameter value). Certainly, additional effects can be envisaged that are not captured by such a minimal model. One example is the possible reversal of cultural practices (in this case farming) by pioneers due to social influences at their destination and/or insufficient numbers of pioneers, which would effectively reduce dispersal at the longest distances considered in our ethnographic kernel. However, in our opinion it is reasonable not to introduce such an effect, because: (i) the reversal of farming into hunting-gathering is a very strange transition that has been very rarely

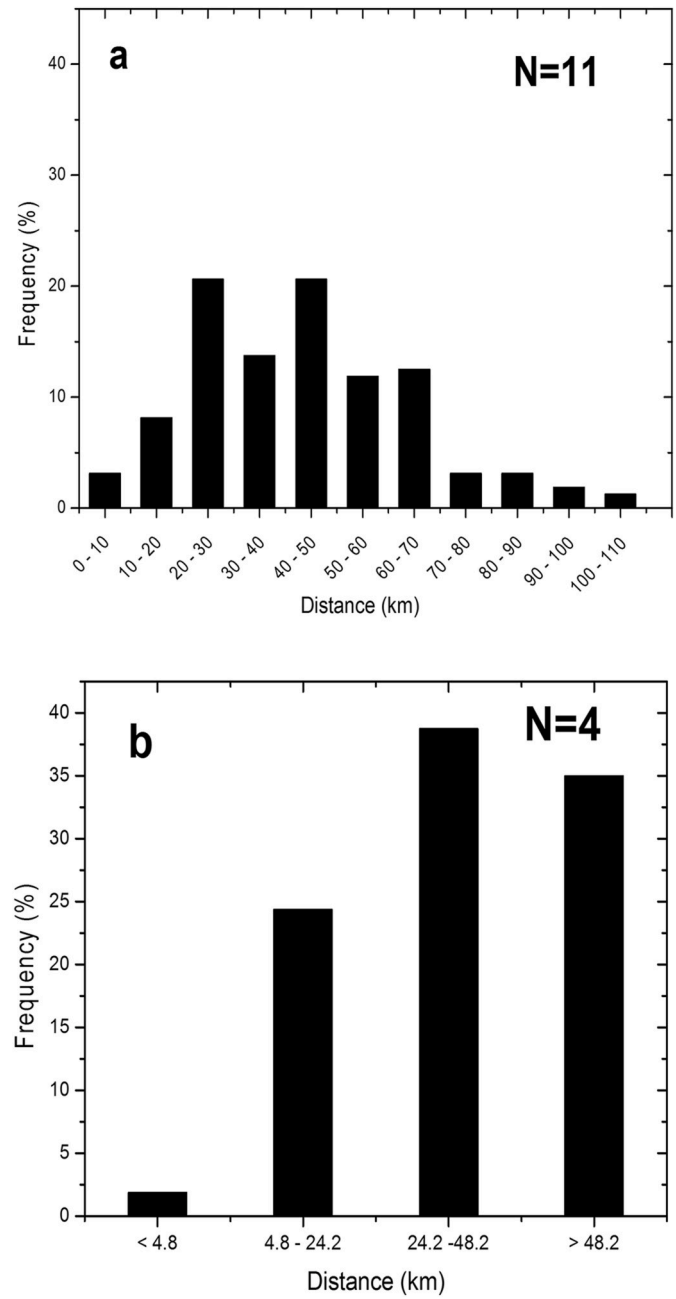

Fig. 3. (a) kernel with $N = 11$ bins, constructed from the 160 individual dispersal distances per generation (Table S1) of a pre-industrial population obtained from the census in Ref. (Biella et al., 1997). When applying Eq. (1) we have used the average distance for each bin, i.e., 5 km, 15 km, …, 105 km. The 11 frequencies or probabilities are (from left to right) $\frac{5}{160}$, $\frac{13}{160}$, $\frac{33}{160}$, $\frac{22}{160}$, $\frac{33}{160}$, $\frac{19}{160}$, $\frac{20}{160}$, $\frac{5}{160}$, $\frac{5}{160}$, $\frac{3}{160}$ and $\frac{2}{160}$. (b) kernel with $N = 4$ bins, also obtained from the 160 individual distances in Table S1. The first three bins have the same distance intervals as the kernels in Ref. (Stauder, 1971), previously used by Ammerman and Cavalli-Sforza (p. 155 in Ref. (Ammerman and Cavalli-Sforza, 1984)) and other authors (e.g., kernels A-C in Ref. (Isern et al., 2008)). For these three bins, when applying Eq. (1) we have used the average distances, i.e., 2.4 km, 14.5 km and 36.2 km (as in Ref. (Isern et al., 2008)). For the fourth bin, we use 72.84 km so that the average distance is the same as for all 160 movements (a similar approach was used for kernels A-C in Ref. (Isern et al., 2008)). The 4 frequencies or probabilities are (from left to right) $\frac{3}{160}$, $\frac{39}{160}$, $\frac{62}{160}$ and $\frac{56}{160}$.

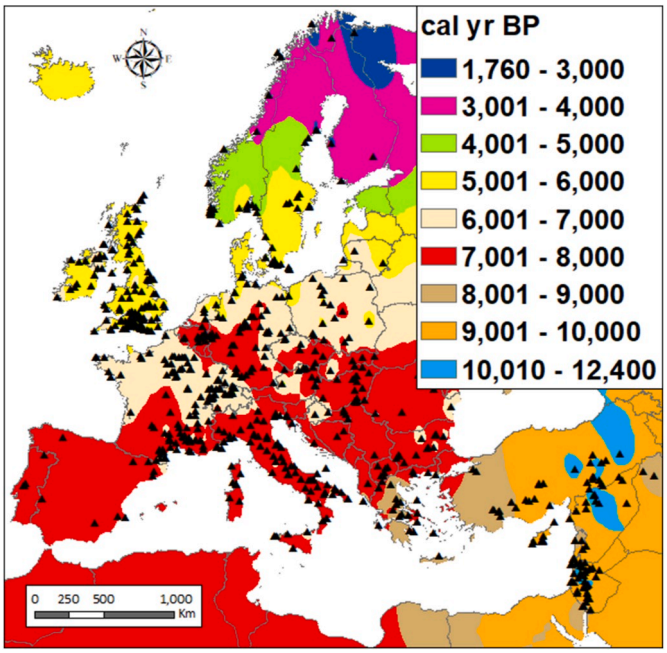

Fig. 4. Interpolation map of calibrated dates of early Neolithic sites in Europe, obtained using Arcmap 10 software. The interpolation method used is Inverse Distance Weighting, but other interpolation methods yield similar results. The database used is that from Ref. (Pinhasi et al., 2005) except in the case of Scandinavia, for which we have applied the database from Ref. (Fort et al., 2018) (the latter it is substantially more complete, because Ref. (Pinhasi et al., 2005) included only Scandinavian sites in Denmark but Ref. (Fort et al., 2018) also includes sites in Sweden, Norway and Finland). It is seen that the spread of the Neolithic in Scandinavia was substantially slower than in continental Europe. For example, from the southern tip of Sweden to the middle of Sweden, the distance is about 1000 km and the time elapsed is about 2000 yr (yellow and green colors), so the spread rate was about 0.5 km/yr. In contrast, from Albania to Switzerland the distance is again about 1000 km but the time elapsed is about 1000 yr (red color), so the spread rate was about 1.0 km/yr.

reported in ethnographic and archaeological work; and, in any case, (i) we are not aware of any ethnographic or archaeological data that allow us to quantity for which distances and with what probabilities it might have existed.

3. First case study: the spread of the Neolithic in continental Europe

Now that we have shown that using histograms (for pre-industrial populations) yields trustable results (i.e., similar to using the complete set of raw distances) for the prediction of Neolithic spread rates, and that the predicted observed rates are consistent with observed one for Europe (Figs. 5a, 6a and 7a), we tackle the question of whether the histogram approach also yields reliable results for the relative importance of demic and cultural diffusion or not.

The cultural effect of a Neolithic wave of advance is defined as the percentage of cultural diffusion in its spread rate, i.e. (Fort, 2012),

$$\%\ cultural\ effect = \frac{s - s_{demic}}{s} \cdot 100 \qquad (2)$$

where s is the speed predicted by Eq. (1) for a given value of the intensity C of cultural diffusion, and s_{demic} is the front speed predicted by the purely demic model (no cultural diffusion), i.e., by Eq. (1) with $C = 0$. Analogously to Eq. (2), the percentage of demic diffusion is $\frac{s_{demic}}{s} \cdot 100$, i.e., 100% minus the percentage of cultural diffusion given by Eq. (2).

In Fig. 5b we plot the cultural effect as a function of C for the complete set of 160 individual intergenerational distances (included as

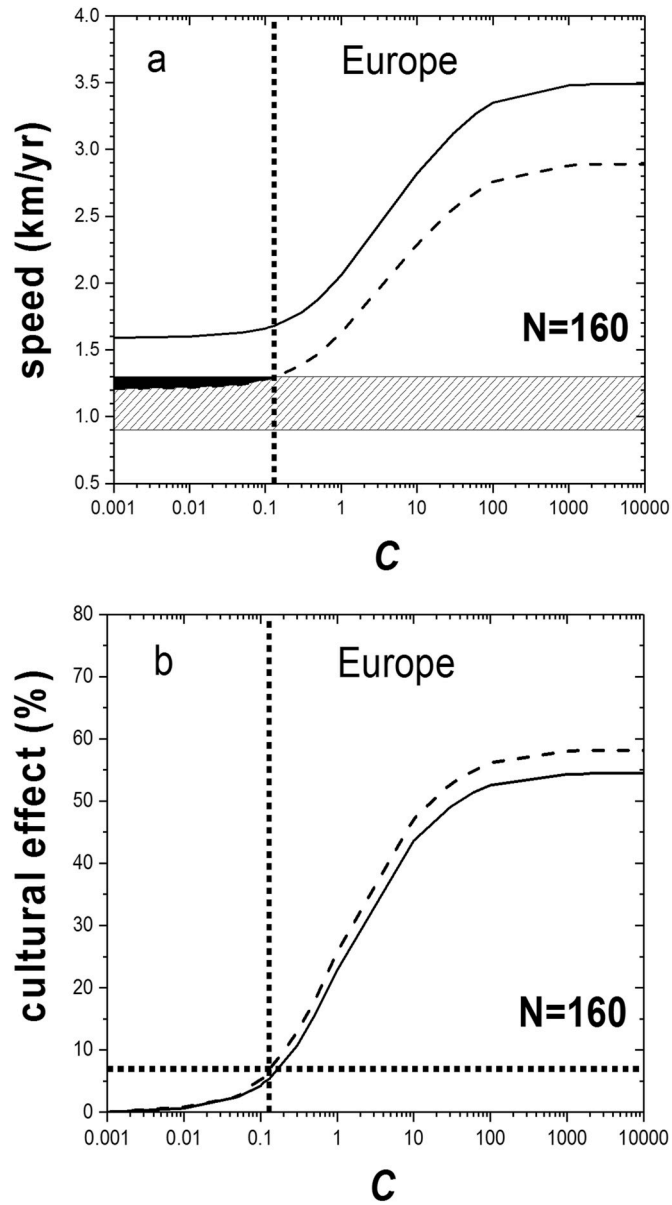

Fig. 5. (a) shows the spread rate (in km/yr) of the Neolithic wave of advance in Europe, obtained from Eq. (1), as a function of the cultural transmission intensity C, using the complete set of individual intergeneration dispersal distances for a pre-industrial population ($N = 160$). The horizontal hatched rectangle is the spread rate implied by the archaeological data (0.9–1.3 km/yr). (b) shows the corresponding percentage of cultural diffusion, obtained from Eq. (2). The percentage of demic diffusion is 100% minus the cultural effect shown in this plot.

Supp. Info. Table S1), i.e., by using the values of s (as a function of C) and s_{demic} from Fig. 5a into Eq. (2). We observe that for the values of C such that there is consistency between the mathematical model and the archaeological data ($C \leq 0.13$, from Fig. 5a), Fir. 5b implies that the cultural effect is below 7%. This indicates that the spread of the Neolithic in Europe was overwhelmingly dominated by demic diffusion, which was responsible for at least 93% of the spread rate. This conclusion, i.e. the primacy of demic over cultural diffusion in the propagation of the Neolithic in Europe, was reached by combining a mathematical model and archaeology in Ref. (Fort, 2012) (but using less detailed dispersal data, i.e., not a complete set of individual dispersal distances) and has been confirmed using genomic data (Mathieson et al., 2015).

It is also of interest to see if the histograms (derived from complete

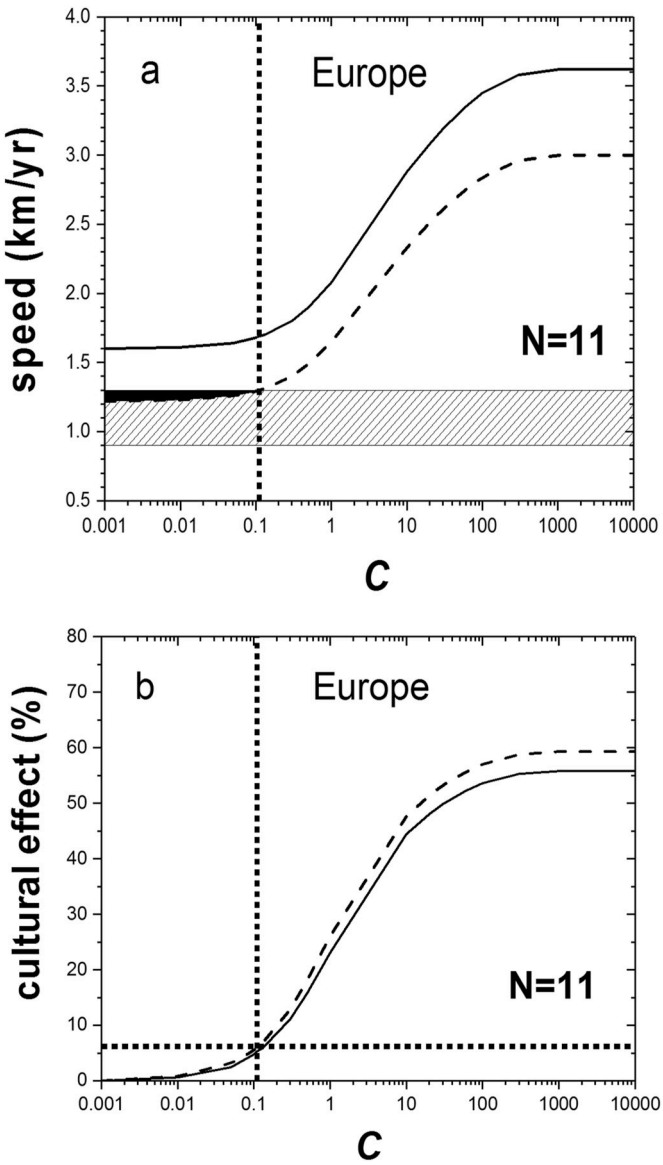

Fig. 6. (a) shows the spread rate (in km/yr) of the Neolithic wave of advance in Europe, obtained from Eq. (1), as a function of the cultural transmission intensity C, using the histogram with $N = 11$ bins computed from the complete set of individual intergeneration dispersal distances for a pre-industrial population (Fig. 3a). The horizontal hatched rectangle is the spread rate implied by the archaeological data (0.9–1.3 km/yr). (b) shows the corresponding percentage of cultural diffusion, obtained from Eq. (2). The percentage of demic diffusion is 100% minus the cultural effect shown in this plot.

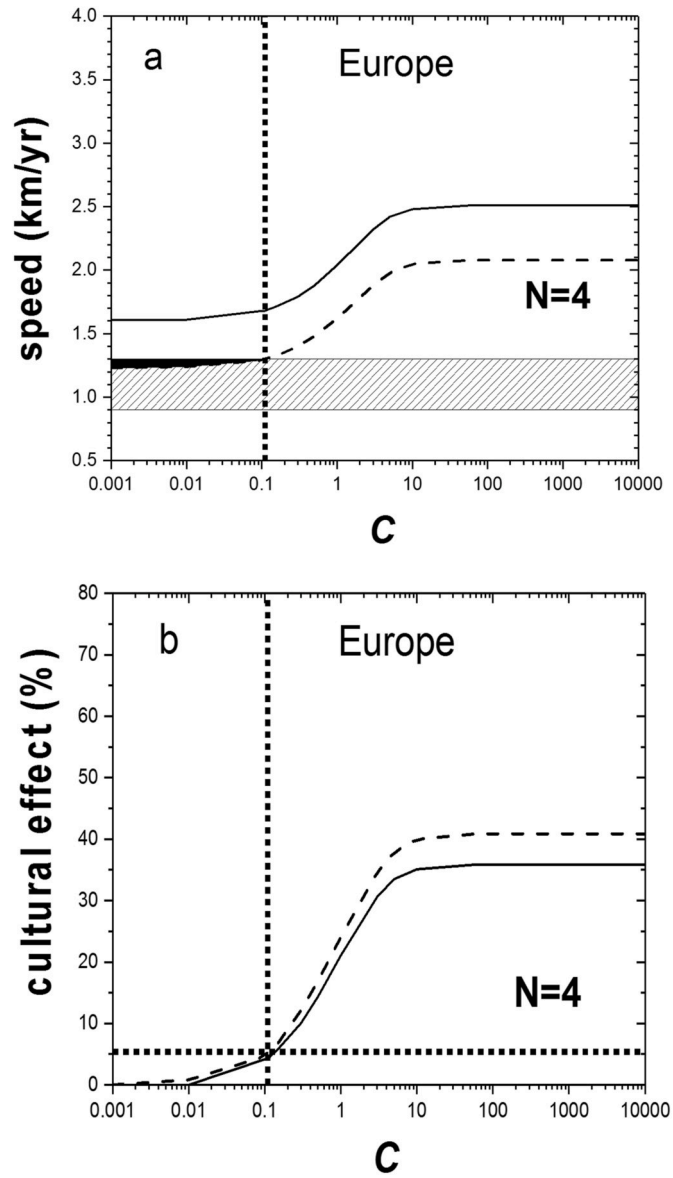

Fig. 7. (a) shows the spread rate (in km/yr) of the Neolithic wave of advance in Europe, obtained from Eq. (1), as a function of the cultural transmission intensity C, using the histogram with $N = 4$ bins computed from the complete set of individual intergeneration dispersal distances for a pre-industrial population (Fig. 3b). The horizontal hatched rectangle is the spread rate implied by the archaeological data (0.9–1.3 km/yr). (b) shows the corresponding percentage of cultural diffusion, obtained from Eq. (2). The percentage of demic diffusion is 100% minus the cultural effect shown in this plot.

set of 160 raw distances in Table S1) provide a reasonable description or not (because if they did not, then all previous work on mathematical Neolithic spread models would have been based on wrong parametrizations, so the results would not be valid). In Fig. 6b we can see that for the histogram with $N = 11$ bins the results are almost the same as for all $N = 160$ distances (Fig. 5b), i.e., the cultural effect is again below 7%. Even for the very simplified histogram for only $N = 4$ bins (Fig. 7b), we see that the cultural effect is very small (below 6%), so the conclusion that the Neolithic spread in Europe was dominated by demic diffusion can be reached even using this very simple histogram. Note that this happens in spite of the fact that, for high values of C, the histogram with $N = 4$ bins (Fig. 7b) yields speeds between 2.1 km/yr and 2.5 km/yr, i.e. substantially slower than the corresponding ranges for the complete set of $N = 160$ distances (2.9–3.5 km/yr, from Fig. 5b) or $N = 11$ bins (3.0–3.6 km/yr, from Fig. 6b).

These results can be viewed as comforting, because after decades of work on Neolithic spread models using histograms (e.g., Ammerman and Cavalli-Sforza, 1984; Isern et al., 2008; Fort, 2012, 2015; Fort et al., 2018) we have now shown (using a database of individual distances) that histograms are a reasonable description, in spite of the long-distance effect previously observed in Ecology, and even if using only $N = 4$ bins.

4. Second case study: the spread of the Neolithic in Scandinavia

The map in Fig. 4 shows clearly that the spread of the Neolithic in Scandinavia was much slower than in continental Europe. This slowness in Scandinavia was discovered recently (Fort et al., 2018) and came as at surprise, given that previous studies (Rowley-Cowney et al., 2013;

Shennan, 2018) had observed qualitatively that the spread of the Neolithic in Scandinavia was rapid (due to the fact that the authors of Refs. (Rowley-Cowney et al., 2013; Shennan, 2018) could compare dates of sites in the southern half of Scandinavia only).

The case of Europe was studied in Ref. (Pinhasi et al., 2005), where it was shown that great-circle distances (i.e., distances over the Earth surface, considered a sphere) yield for the spread rate the range 0.9–1.1 km/yr, whereas shortest-path distances (which, in general, take into account the effects of landscape, vegetation, etc.) yield 1.1–1.3 km/yr. Thus we have used 0.9–1.3 km/yr (Fort, 2012) for the overall range in Europe (hatched rectangle in Figs. 2, 5a and 6a and 7a). Similarly, the case for Scandinavia was studied in Ref. (Fort et al., 2018), where it was shown that great-circle distances yield 0.44–0.66 km/yr, whereas shortest-path distances yield 0.56–0.84 km/yr. Thus we use 0.44–0.84 km/yr for the overall range in Scandinavia (hatched rectangle in Fig. 8a).

The curves in Fig. 8a have been obtained using Eq. (1) and the complete kernel with $N = 160$ distances (Supp. Info., Table S1), with the range of the generation time T given below Eq. (1) and the range $0.0069 \leq a \leq 0.0190$ yr^{-1} for the initial growth rate (as estimated in Ref. (Fort et al., 2018) from Scandinavian archaeological data). We see that also for Scandinavia, there is consistency (black area) between the spread rates predicted by the model (area between the two curves) and those determined from archaeological data (hatched rectangle). For Scandinavia the cultural effect, given by Eq. (2), is shown in Fig. 8b, where we see that it is below 19%, so we can conclude that also in Scandinavia the Neolithic spread mainly due to demic diffusion, although possibly with a higher percentage of cultural diffusion than in mainland Europe (because the cultural effect in the previous section is below 7%). This conclusion was reached previously with less detailed dispersal data (i.e., not using a complete set of individual distances) (Fort et al., 2018) and agrees with genomic data (Mittnik et al., 2018; Skoglund et al., 2012, 2014; Malmström et al., 2015). Genetics cannot, however, determine the percentages of demic and cultural diffusion on the spread rate, because the latter is a purely archaeological (not genetic) feature. In Supp. Info., text S1, we include the results for Scandinavia using the complete raw dispersal data ($N = 160$ distances, Fig. S1) and using the simplified histogram ($N = 4$ bins, Fig. S3) and they are very similar to Fig. 8 ($N = 11$ bins).

The two main new conclusions from these two case studies (Secs. 3 and 4) are the following. (i) We have shown explicitly that using the complete set of intergenerational distances for a pre-industrial population (as done here for the first time) yields spread rates consistent with the archaeological record, both for continental Europe and for Scandinavia, in spite of the fact that the spread across Scandinavia was clearly slower (Fig. 4). (ii) Not only for mainland Europe (Sec. 3) but also for Scandinavia, the exact results (i.e., those obtained from the complete set of $N = 160$ distances) are very similar to those using histograms obtained from the complete set. This is true for histograms with $N = 11$ bins and even only $N = 4$ bins, and both for the spread rate and the percentages of demic and cultural diffusion. Both conclusions (i) and (ii) place Neolithic spread models on a more solid ground than up to now, since the validity of histograms had been never established by comparing to a complete set of individual distances.

5. Additional case studies: specific Neolithic cultures in Europe

Bocquet-Appel and co-workers estimated the spread rate for several ceramic cultures in Europe (Bocquet-Appel et al., 2009, 2012). They considered the following inland cultures (Bocquet-Appel et al., 2012): (1) Painted Pottery (PP), including Starcevo, Koros, Cris, Proto-Sesklo, Karanovo and Chadvar-Kremikovci; (2) LinearBandKeramik (LBK), which they grouped together with Eastern Linear Pottery (ELP) because they could not perform a statistically sound analysis for ELP alone due to its small geographical region (and LBK is the most similar and geographically nearest culture to ELP); and (3) Trichterbeckerkultur

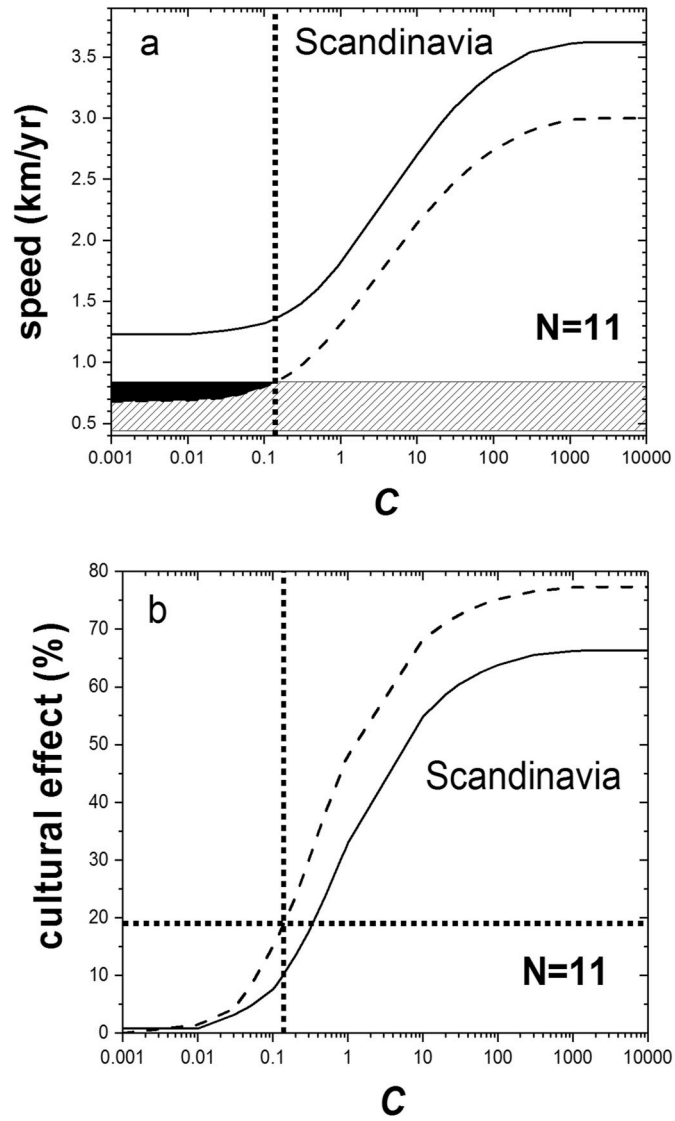

Fig. 8. (a) shows the spread rate (in km/yr) of the Neolithic wave of advance in Scandinavia, obtained from Eq. (1), as a function of the cultural transmission intensity C, using the histogram with $N = 11$ bins computed from the complete set of individual intergeneration dispersal distances for a pre-industrial population (Fig. 3a). The horizontal hatched rectangle is the spread rate implied by the archaeological data (0.44–0.84 km/yr). (b) shows the corresponding percentage of cultural diffusion, obtained from Eq. (2). The percentage of demic diffusion is 100% minus the cultural effect shown in this plot. Similar plots for Scandinavia with $N = 160$ and $N = 4$ are included in Supp. Info., Figs. S1 and S3, respectively.

(TRBK). According to the map by Bocquet-Appel et al. (Ref. (Bocquet-Appel et al., 2012), Fig. 2), the PP sites in their database are apparently located in Greece, the Balkans, Bulgaria and Romania; immediately to the North of them lies the ELP area (mainly Hungary and Slovakia), to the west of ELP begins the LBK area (mainly Austria, Germany and northern France), and finally their TRBK sites are located North of both the ELP and the LBK regions (apparently in Czechia, Poland, northern Germany and Denmark). Therefore, as noted in Ref. (Bocquet-Appel et al., 2012), these 3 ceramic cultures span all of Europe along a southeast-northwest axis across the center of Europe.

Bocquet-Appel et al., 2009, 2012 divided the continent in 70 × 70 km grid squares, interpolated a surface (giving the date of first arrival) to the average of the two earliest Neolithic dates in each grid square, and estimated the spread rate and direction at each square. They noted that

extreme (i.e., very fast) values of the speed in some grid squares may have biased their results (indeed, some standard deviations in their Table 2 are larger than the corresponding averages). We agree that such extreme values are probably unrealistic artifacts, and may be due to side effects, the paucity of data in some regions, etc. Therefore, it seems cautious to estimate the speed range for each culture by keeping only the central part of its probability distribution (as plotted in Ref. (Bocquet-Appel et al., 2012), Fig. 10). We have done so by dividing the maximum probability of each plot (culture) by 10, and considering the distribution within the corresponding range (in this way, we retain more than 85% of the area under each distribution). Then the distributions (Ref. (Bocquet-Appel et al., 2012), Fig. 10) lead to the speed ranges (1) 0–1.7 km/yr for PP; (2) 0–1.6 km/yr for LBK and ELP; and (3) 0–1.2 km/yr for TRBK. An estimation for LBK alone is also possible (by using the probability distribution in Ref. (Bocquet-Appel et al., 2012), Fig. 8) and yields 0–1.7 km/yr, i.e., the same as for PP. An independent map of spread rates (Fig. 3 in Ref. (Fort, 2015)) agrees with the fact that the PP and LBK are have essentially the same speed, and also with the observation that the TRBK area displays clearly slower speeds than the PP and LBK regions.

As noted above for overall Europe (Figs. 5–7) and Scandinavia (Fig. 8), the relevant speed value to estimate the percentage of demic and cultural diffusion is the upper limit of the speed range estimated from archaeological data (i.e., the upper side of the dashed rectangle in Figs. 5a–8a). For this reason, we can compare the three cultures considered above in a single plot (Fig. 9a, where the two curves are the same as in Fig. 5), without loosing clarity, by including only the upper speed value for each of the three cultures, i.e., (1) 1.7 km/yr for PP, horizontal dotted line in Fig. 9a; (2) 1.6 km/yr for LBK and ELP, horizontal dashed line in Fig. 9a; and (3) 1.2 km/yr for TRBK, horizontal dashed-dotted line in Fig. 9a. Note that all three ranges for the speed are consistent with the model (area between the two curves), but only slightly for TRBK (because of its slowness). Using the values from Fig. 9a into Eq. (2), as already done in Fig. 5, we plot the cultural effect in Fig. 9b, which yields the following cultural effects for the three cultures considered: (1) 0–28% for PP; (2) 0–24% for LBK and EPL; and (3) 0% for TRBK. Therefore, we conclude that all of these results imply that cultural diffusion had a less important role than demic diffusion in the spread of Neolithic cultures in Europe (because all cultural effects are below 50%).

For completeness, we would like to add that two situations that are of interest but have not been considered in this paper.

(i) In some regions (including possibly part of the TRBK spread), the speed could have been even slower than the values reported above. One possible explanation might be a substantial reduction of dispersal distances due to strong cultural diffusion effects. This has been suggested by some genetic and ethnographic data, but unfortunately the corresponding kernels have not been measured yet (see Ref. (Fort, 2012), Supp. Info., Sec. S6). Another possible reason is a lower growth rate (similarly to Scandinavia, see Sec. 4 above).

(ii) Bocquet-Appel et al. (2012) also considered some cultures distributed along the coast, which display faster spread rates (Bocquet-Appel et al., 2012). Similarly to situation (i) above, we think that the kernels used in the present paper are invalid for such cultures. For example, for the case of the Western Mediterranean it has been shown that characteristic dispersal distances of at least 300 km per generation are necessary to explain the very fast observed rate (8.7 km/yr) (Isern et al., 2017a). However, such distances are clearly much longer that those of all pre-industrial kernels so far reported (e.g., Table S1 and Fig. 3a and b in the present paper). Unfortunately we are not aware of any ethnographic, archaeological or genetic data that make it possible to measure the dispersal kernel of pre-industrial coastal populations of farmers, and this is the reason why we have focused on inland cultures.

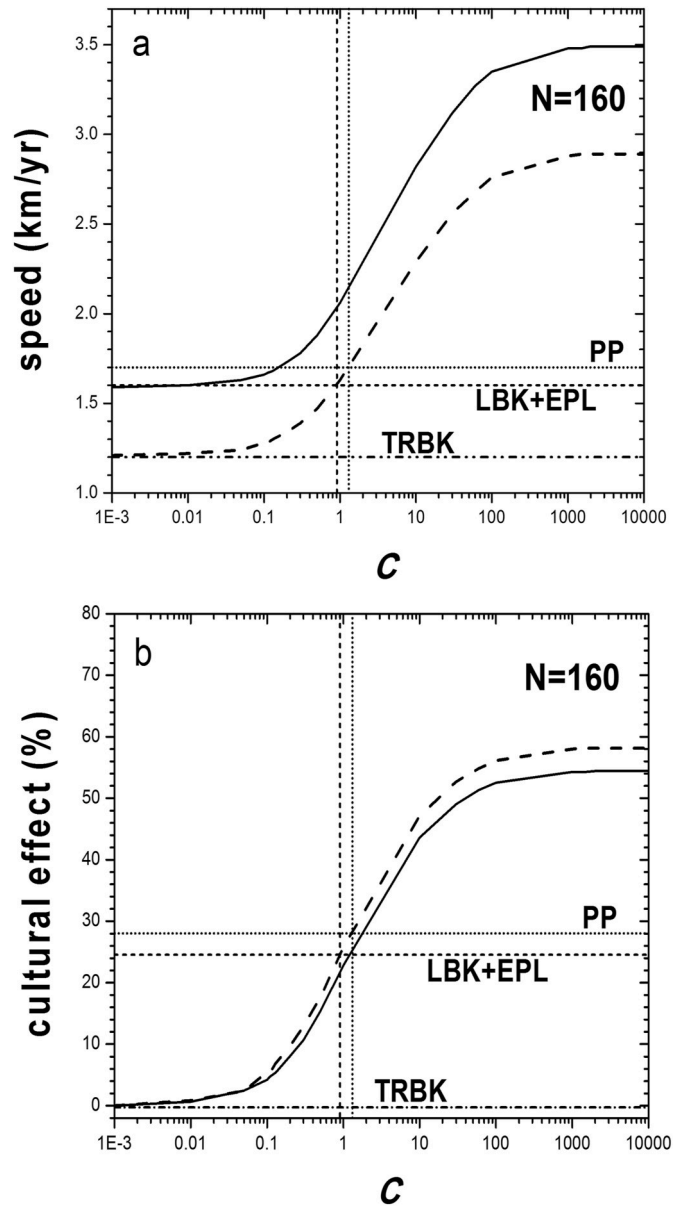

Fig. 9. The curves in these plots are the same as in Fig. 5, but here they are applied to three regional Neolithic cultures in Europe, namely Painted Pottery (PP), the complex formed by LinearBandKeramik (LBK) and Eastern Linear Pottery (ELP), and Trichterbeckerkultur (TRBK). For each culture, the horizontal line in (a) gives the upper bound of its observed spread rate, and (b) makes it possible to estimate the range of the effect of cultural diffusion.

Just to summarize, in this paper we have considered the case studies for which it seems possible to estimate the necessary model parameters. In other case studies the speed was either very fast (due to coastal spread) or very slow (perhaps due to strong acculturation and/or slower population growth). If in future work it were possible to obtain direct estimations of the corresponding dispersal kernels and/or initial growth rates, it would be of interest to apply our method to such additional case studies.

6. Discussion and conclusions

Dispersal data of human populations are published in histograms,

their longest-distance class usually being labelled as '>50 km' or '>100 km' (see, e.g., Fig. 5.8 in Ref. (Ammerman and Cavalli-Sforza, 1984)). In contrast, the detailed dispersal histogram by Boyce et al. (1971) (Fig. 1) exhibits substantially longer distances (up to about 600 km), which lead to strong long-distance dispersal effects and too fast spread rates to agree with the archaeological record of early Neolithic Europe (Sec. 2.1 and Fig. 2a). Such long distances (up to about 600 km) are presumably due to the fact that mechanized forms of transport led to a dramatic increase in dispersal in mid-nineteenth century in Europe (Boyce et al., 1971). Although it is very difficult to find sufficiently detailed kernels, Ref. (Dodinval, 1973) reports another industrialized population which also exhibits long distances (above 250 km).

In contrast, in Sec. 2.2 we have seen that the maximum distance of a pre-industrial population is substantially shorter (about 100 km), so such long-dispersal events do not arise. Using the corresponding dispersal data into Neolithic spread models yields spread rates that are consistent with the archaeological record (Figs. 5–8). This strongly suggests that pre-industrial modern populations are a reasonable proxy to parametrize dispersal kernels in Neolithic spread models.

We have been able to determine the maximum dispersal distance of a pre-industrial population because we have used, for the first time, the individual distances (rather than histograms, i.e. probabilities for distance ranges) of a pre-industrial population.

Since the development of the first Neolithic spread models, it was noted that dispersal data are substantially more difficult to estimate than reproductive data (Ammerman and Cavalli-Sforza, 1973). Here we have shown that long-distance dispersal effects, which are well-known from Ecology (Clark, 1998), arise when using dispersal data from industrialized populations (Fig. 2). The results of the present paper establish the validity of Neolithic spread models, but only if they are parametrized by means of carefully selected dispersal data, in the sense that data from industrialized populations should be avoided and, instead, pre-industrial populations should be used. We stress that this is the only possibility at present, because direct measurement of dispersal kernels for prehistoric populations have never been performed (strontium isotope and other techniques do not yield sufficiently precise distances), although it has been proposed that genetic approaches could be used for this purpose in the future (Fort, 2015).

An unexpected, nice result from the present paper is that when using the complete set of distances for pre-industrial farmers to estimate dispersal kernels, we obtain similar quantitative results (both for the spread rate and the cultural effect) than using the complete set, even if histograms with only 4 bins are applied (Figs. 5–7 for Europe; Fig. 8 and S1-S3 for Scandinavia). This puts Neolithic spread models based on histograms on a substantially firmer ground than up to now.

Using linear regression, or simply looking at an interpolation map (Fig. 4), it is noted that the spread rate of the Neolithic in Europe was about 1 km/yr (Sec. 3) and, in contrast, in Scandinavia it was substantially slower, about 0.5 km/yr (Sec. 4). However, both cases are explained by Neolithic spread models provided that use is made of dispersal data from pre-industrial populations (as well as of the net reproductive rates implied by independent observations for each case). This indicates that pre-industrial populations are probably an appropriate source of mobility data for Neolithic spread models, if adequate and careful parametrization is performed. The analyses reported confirm that demic diffusion was more important than cultural diffusion in both case studies. The same analysis for the spread of regional Neolithic cultures is also possible (Sec. 5), except in cases in which dispersal kernels have not yet been estimated from real data, e.g., for instances of coastal spread (whih lead to fast spread rates, such as in the western Mediterranean) and strongly acculturating populations (which could lead to slow spread rates, and this might include the TRBK culture). In the latter cases (slow speeds), an alternative explanation may be low initial growth rates, and this possibility could be tested archaeologically (similarly to Scandinavia).

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jas.2020.105148.

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