Synthesis between demic and cultural diffusion in the Neolithic transition in Europe

Joaquim Fort[1]

Complex Systems Laboratory, Department of Physics, University of Girona, ES-17071 Girona, Catalonia, Spain

Edited by Marcus W. Feldman, Stanford University, Stanford, CA, and accepted by the Editorial Board October 2, 2012 (received for review January 12, 2012)

There is a long-standing controversy between two models of the Neolithic transition. The demic model assumes that the Neolithic range expansion was mainly due to the spread of populations, and the cultural model considers that it was essentially due to the spread of ideas. Here we integrate the demic and cultural models in a unified framework. We show that cultural diffusion explains ~40% of the spread rate of the Neolithic transition in Europe, as implied by archaeological data. Thus, cultural diffusion cannot be neglected, but demic diffusion was the most important mechanism in this major historical process at the continental scale. This quantitative approach can be useful also in regional analysis, the description of Neolithic transitions in other continents, and models of many human spread phenomena.

fronts | cultural transmission | reaction-dispersal | reaction-diffusion

The Neolithic transition, a major episode in human history, is defined as the shift from a hunter-gatherer economy (Paleolithic) into another one based on agricultural activities (Neolithic) (1). In the Near East, this transition took place ~12,000 y ago, and from there it spread across Europe until ~5,000 y ago (2–4). Archaeologists have provided many data that make it possible to measure the speed of the spread of the Neolithic transition, but they disagree on which of the following possibilities is correct: (*i*) it was mainly a demic process (range spread of farmers) (5); (*ii*) it was mainly a cultural one (transmission of the plants, animals and knowledge of farmers to hunter-gatherers (6)); or (*iii*) it was mainly demic in some regions and mainly cultural in others (7). It is important to note that many authors have clearly argued for the importance of both demic and cultural diffusion. For example, Ammerman and Cavalli-Sforza (8), when introducing their demic diffusion model in 1973, wrote that demic and cultural diffusion are not mutually exclusive, and discussed the interactions between the Neolithic and Paleolithic populations that would have led to cultural diffusion and genetic clines. These authors also made some crucial statements: "The real question may well be to evaluate the relative importance of demic and cultural diffusion in different regions of Europe" because "in some areas both are likely to have contributed to the spread of farming," but "what is necessary before such an attempt can be made is the introduction of much more specific models" (ref. 4, pp. 6, 135, and 62, respectively). This is precisely the problem to which the present paper aims to contribute: we will here present a model, and apply it to determine the importance of demic and cultural diffusion on the spread rate at the continental scale. We will also outline how our model could be applied to solve the same problem at regional scales in future work.

Several aspects of transitions in human prehistory have been analyzed during the past decade using increasingly refined mathematical models (9–16). On the other hand, genetic studies have led to an increasing consensus that demic dispersal was important in the Neolithic transition in Europe (17, 18). However, our purpose in this paper is not to analyze the origin and spread of genes. Instead, we ask a different question: What do the archaeological data tell us on the relative importance of demic and cultural diffusion on the spread rate of the Neolithic front? An advantage of focusing our attention on the spread rate (not on the genes) is that it makes direct quantitative comparisons to archaeological data possible. However, up to now, mathematical models of population spread (9–16) have not been applied to the controversy between the demic and cultural models of the Neolithic transition. Can a mathematical model, based on anthropologically realistic principles, shed some light on the relative importance of the demic and cultural contributions to the spread rate of the Neolithic transition? Here we will show that the answer to this question is affirmative, by integrating demic models with cultural transmission theory in a unified framework.

Results

To focus on the effects of cultural transmission, consider first homogeneous systems (i.e., such that the population densities do not depend on position). Let P_N stand for the total number of Neolithic farmers and P_P for the total number of Paleolithic hunter-gatherers. The evolution equations are (*Methods*)

$$\begin{cases} P'_N = P_N + f\dfrac{P_N P_P}{P_N + \gamma P_P}, \\ P'_P = P_P - f\dfrac{P_N P_P}{P_N + \gamma P_P} \end{cases} \qquad [1]$$

where the primes denote after the effect of cultural transmission. The positive and negative signs correspond to the fact that the transmission of the cultural trait (agriculture) increases the number of farmers and decreases that of hunter-gatherers. The parameter f in Eq. **1** is the intensity of cultural transmission, and the interpretation of γ is as follows. If $\gamma < 1$, then γ is a measure of the preference by hunter-gatherers to copy the behavior of farmers rather than that of other hunter-gatherers (conversely, if $\gamma > 1$ hunter-gatherers prefer to copy other hunter-gatherers rather than farmers; *Methods*). In contrast to Lotka-Volterra (4, 12, 19) or other (16) equations for interacting populations, the evolution Eq. **1** has been derived from cultural transmission theory (20) (*Methods*). In *Frequency-Dependent Cultural Transmission*, we include an explanation on why more complicated, frequency-dependent models are not necessary for our purposes.

To analyze the spatial dynamics of the Neolithic spread, we need to extend this framework to nonhomogeneous systems. We will not take into account geographical factors (mountains, sea travel, etc.), because they have been recently shown to have a small effect at the continental scale in purely demic models (3). Let $N(x,y,t)$ and $P(x,y,t)$ stand for the local population densities (per unit area) of Neolithic farmers and Paleolithic hunter-gatherers,

---

Author contributions: J.F. designed research, performed research, analyzed data, and wrote the paper.

The author declares no conflict of interest.

This article is a PNAS Direct Submission. M.W.F. is a guest editor invited by the Editorial Board.

[1] E-mail: joaquim.fort@udg.edu.

This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1200662109/-/DCSupplemental.

respectively, at position (x,y) and time t. As is shown in *Methods*, the simplest nonhomogenous generalization of Eq. **1** is the following set of coupled reaction-diffusion equations:

$$\begin{cases} \dfrac{\partial N}{\partial t} = D_N \nabla^2 N + F(N) + \dfrac{f}{T}\dfrac{NP}{N+\gamma P} \\ \dfrac{\partial P}{\partial t} = D_P \nabla^2 P + F(P) - \dfrac{f}{T}\dfrac{NP}{N+\gamma P} \end{cases}, \tag{2}$$

where D_N and D_P are the diffusion coefficients of the N and P populations, respectively, $F(N) = a_N N\left(1-\frac{N}{K_N}\right)$ and $F(P) = a_P P\left(1-\frac{P}{K_P}\right)$ are logistic functions describing net reproduction (with a_i the initial growth rate and K_i the carrying capacity of population $i =$ N, P), and T is the generation time (defined as the mean time interval between the migration of an individual and one of her/his children (21) and roughly the same for both populations (22)]. Logistic growth functions are well-known to agree with many population data for humans (ref. 9 and references therein). Fisher's equation is obtained from Eq. **2** if $f = 0$. Fisher's equation was used by Ammerman and Cavalli-Sforza in their demic diffusion model (4, 8). However, in recent years it has been shown that reaction-diffusion equations can lead to substantial errors for human populations due to two special features of human mobility: (*i*) the effect of realistic human dispersal kernels is important and leads to the breakdown of the diffusion approximation (11), and (*ii*) humans need to spend some time with their parents before being able to disperse and survive on their own (cohabitation effect) (23). Taking both effects properly into account, Eq. **2** is replaced by the more realistic set of integrodifference, discrete-time equations (*Methods*)

$$\begin{cases} N(x,y,t+T) = \displaystyle\int_{-\infty}^{\infty}\int_{-\infty}^{\infty} \tilde{N}(x+\Delta_x, y+\Delta_y, t)\,\phi_N(\Delta_x,\Delta_y)\,d\Delta_x\,d\Delta_y \\ P(x,y,t+T) = \displaystyle\int_{-\infty}^{\infty}\int_{-\infty}^{\infty} \tilde{P}(x+\Delta_x, y+\Delta_y, t)\,\phi_P(\Delta_x,\Delta_y)\,d\Delta_x\,d\Delta_y \end{cases}, \tag{3}$$

where

$$\tilde{N}(x,y,t) \equiv R_T[N(x,y,t)] + f\frac{R_T[N(x,y,t)]R_T[P(x,y,t)]}{R_T[N(x,y,t)] + \gamma R_T[P(x,y,t)]}$$

$$\tilde{P}(x,y,t) \equiv R_T[P(x,y,t)] - f\frac{R_T[N(x,y,t)]R_T[P(x,y,t)]}{R_T[N(x,y,t)] + \gamma R_T[P(x,y,t)]}, \tag{4}$$

$R_T[N(x,y,t)] = \frac{e^{a_N T} K_N N(x,y,t)}{K_N + (e^{a_N T}-1)N(x,y,t)}$, and $R_T[P(x,y,t)] = \frac{e^{a_P T} K_P P(x,y,t)}{K_P + (e^{a_P T}-1)P(x,y,t)}$ are the new population densities due to logistic net reproduction during the time interval T, and $\phi_i(\Delta_x, \Delta_y)$ is the dispersal kernel of population $i =$ N, P.

As shown in *Methods*, when population N expands its range into a space occupied by population P, and their population densities evolve according to Eqs. **3** and **4**, the front speed is

$$s = \min_{\lambda>0} \frac{a_N T + \ln\left[(1+C)\left(\sum_{j=1}^{M} p_j I_0(\lambda r_j)\right)\right]}{T\lambda}, \tag{5}$$

where, interestingly, the cultural transmission parameters f and γ do not appear separately but combined in their ratio, $C = \frac{f}{\gamma}$. In our opinion, this combination is a nice result because of its simplicity and because it has a clear interpretation: C is the average number of hunter-gatherers converted by each farmer per generation at the leading edge of the wave of advance, i.e., for $N << P$ (*Methods*). Finally, p_j is the probability of the N individuals to disperse at distance r_j $(j = 1, 2, \ldots, M)$, and $I_0(\lambda r_j) = \frac{1}{2\pi}\int_0^{2\pi} d\theta \exp[-\lambda r_j \cos\theta]$ is the modified Bessel function of the first kind and order zero.

According to ethnographic reports, farming is rarely copied at large distances by hunter-gatherers (24, 25). Accordingly, we do not include nonlocal cultural transmission here; however, taking it into account would not change our conclusions as long as we use parameter values estimated from empirical data (*Nonlocal Cultural Transmission*).

To apply Eq. **5** we use the following parameter ranges, as obtained from ethnographic and archaeological observations (*Parameter Values and Observed Neolithic Front Speed Range*), $0.023\ y^{-1} \le a_N \le 0.033\ y^{-1}$, $29 \le T \le 35$ y, $1.0 \le C \le 10.9$, and the following probabilities and distances for the dispersal kernel: $\{p_j\} = \{0.42; 0.23; 0.16; 0.08; 0.07; 0.02; 0.01; 0.01\}$, $\{r_j\} = \{2.3; 7.3; 15; 25; 35; 45; 55; 100\}$ km. Other realistic kernels for preindustrial farmers yield similar results (*Parameter Values and Observed Neolithic Front Speed Range*). Using these ranges into Eq. **5** we obtain Fig. 1, which plots the maximum and minimum Neolithic front speeds (full and dashed curves, respectively). Also in Fig. 1, the observed speed range of the Neolithic transition in Europe is shown by the hatched horizontal rectangle and has been obtained from archaeological data (*Parameter Values and Observed Neolithic Front Speed Range*). The observed range of the conversion intensity C of agriculture from farmers to hunter-gatherers corresponds to the hatched vertical rectangle and has been obtained from anthropological data (*Parameter Values and Observed Neolithic Front Speed Range*). For $1 \le C \le 2.5$ (black area in Fig. 1), the predicted speed range (i.e., that between the dashed and full curves) is seen to be consistent with the observed speed range (hatched horizontal rectangle). Finally, in Fig. 1, we observe that the speed has a finite limit s^* as $C \to \infty$, which is simply the maximum possible speed for individuals

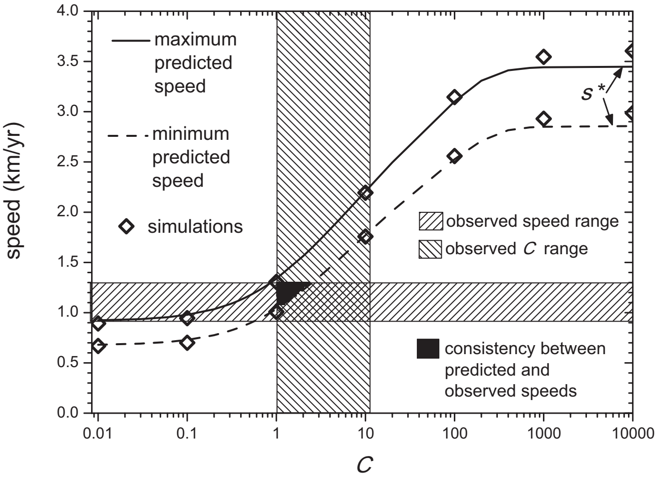

Fig. 1. Predicted Neolithic front speeds. The maximum speed (full curve) has been computed using Eq. **5**, the maximum observed value for the growth rate of preindustrial farmers (a_N = 0.033 y^{-1}) and their minimum generation time (T = 29 y). The minimum speed (dashed curve) has been computed using Eq. **5**, the minimum observed value for the growth rate of preindustrial farmers (a_N = 0.023 y^{-1}) and their maximum generation time (T = 35 y). The hatched horizontal rectangle corresponds to the observed speed of the Neolithic front in Europe ($0.9<s<1.3$ km/y). The hatched vertical rectangle corresponds to the observed range of the conversion intensity ($1.0<C<10.9$). Details on the observations leading to these observed ranges of a_N, T, s, and C, as well as to the dispersal kernels of preindustrial farmers, are given in *Parameter Values and Observed Neolithic Front Speed Range*. The symbols are the speeds obtained from numerical simulations of Eqs. **3** and **4** (*Numerical Simulations*).

moving up to a maximum distance Δ_{max} per generation, namely $s^* = \frac{\Delta_{max}}{T}$. For the kernel introduced above, $\Delta_{max} = 100$ km, and we obtain $s^* = 2.857$ km/y for $T = 35$ y and $s^* = 3.448$ km/y for $T = 29$ y, which agree up to the third decimal digit with the values of s^* obtained from Eq. **5** in Fig. 1. This is a useful check of Eq. **5**, and also shows that our Eqs. **3** and **4** are physically more reasonable than the reaction-diffusion model **2**, which predicts an unbounded speed as $C \to \infty$ [for completeness, in *Reaction-Diffusion Model*, we show that the reaction-diffusion model **2** leads to similar results than Eqs. **3** and **4**, so our conclusions do not depend on the use of a dispersal kernel (11), instead of conventional diffusion, or on the cohabitation effect (23)].

Fig. 2 shows the effect of cultural transmission (i.e., the percent difference between the speed in Fig. 1 for the value of C considered and the speed of the purely demic model, $C = 0$, relative to the former). Fig. 2 shows that, for the range implied by the observations in Fig. 1 ($1 \le C \le 2.5$), the cultural effect is 40 ± 8%. Conversely, the demic effect is ∼60%, which implies that, at the continental European scale, the contribution of demic dispersal (spread of populations) was substantially larger (∼50% larger) than that of cultural transmission (spread of ideas). Therefore, demic diffusion was the most important effect driving the Neolithic range expansion in Europe, but the effect of cultural diffusion was also important and cannot be neglected.

Discussion

We stress that this paper does not attempt to answer the question of whether the genes of modern-day Europeans are primarily of Middle Eastern farmer origin. Instead, we have focused on whether the archaeological data imply that the main mechanism responsible for the spread rate was demic or cultural diffusion. To tackle this question, here we have presented a model of culture spread that combines cultural transmission theory with the effects of demic dispersal and population growth. The model is based on physical transport equations and anthropologically realistic assumptions and parameter values, and it leads to an equation for the spread rate of the wave of advance, Eq. **5**, that depends on the number C of hunter-gatherers converted by farmer and generation at the leading edge of the front, which seems reasonable. The model also shows that, at the continental scale, demic diffusion was the most important process responsible for the spread rate of the Neolithic transition in Europe. This framework unifies demic front propagation (23) and cultural transmission theory (20), and also shows how Neolithic transitions are likely to function, driven by a combination of demic and cultural diffusion and amenable to physical modeling. Of course, the 40% contribution of cultural diffusion (as estimated above) is a continental average and will vary spatially. Therefore, the model should be also applied to regional analyses. For example, the Linearbandkeramic (LBK) Neolithic culture in central Europe spread rate has been recently (26) estimated as 0.8 km/y, which is consistent with the curves in Fig. 1 for $C \approx 0$ (0.7–0.9 km/y), implying a very small percentage for the cultural effect (Fig. 2 for $C \approx 0$). This result is encouraging, because the LBK range expansion is widely regarded as demic by archaeologists (27). More detailed analyses of the LBK data will be necessary to estimate the statistical errors in the LBK observed speed and its cultural effect. Similar work should be performed for other inland Neolithic cultures. On the other hand, some local Neolithic speeds were substantially faster (26) but, because sea travel was probably important, simulations in real geographies will be necessary to perform detailed comparisons of our model with such data. Overall, this work opens a way to discriminate the roles of demic and cultural diffusion at regional scales within Europe, as well as for Neolithic transitions in other regions of the world and for other historical transitions and cultural diffusion phenomena. The approach in this paper will be extended elsewhere to include interbreeding. Further specific potential applications include the Austronesian Neolithic expansion (28), many examples of language substitution, crop dispersals (29), etc.

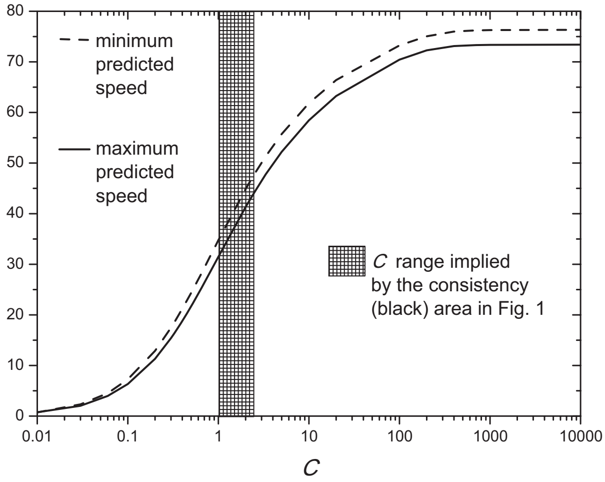

Fig. 2. Cultural effect on the Neolithic front speed, defined as the percent difference between the speed predicted by the demic-cultural model and that predicted by the purely demic model ($C = 0$), relative to the former. This figure shows that, for the range of C consistent with the observed speed in Fig. 1 (hatched rectangle), the effect of cultural transmission on the spread rate of the Neolithic transition in Europe was 40 ± 8%.

Methods

Homogeneous Systems. It is well known from ethnographic studies that hunter-gatherers (P) sometimes become farmers (N), but the reverse transition is very rare (4). Thus, the cultural process P→N will be included in our model, whereas N→P will not. For the number of individuals in the new generation we write

$$\begin{cases} P_N' = P_N + I \\ P_P' = P_P - I \end{cases}, \qquad [6]$$

where $I \ge 0$ (the interaction term) is the number of hunter-gatherers becoming farmers per generation.

Special case. A derivation (20) for the interaction term I under cultural transmission introduces n as the number of teachers (other than parents) that a P individual contacts during his/her lifetime. This derivation also assumes that, of these n teachers, a proportion $u = \frac{P_N}{P_N + P_P}$ is of type N, so the number of teachers of type N is $nu = n\frac{P_N}{P_N + P_P}$ (in the next paragraph, we drop this assumption and generalize this model). If g is the probability that a P individual becomes N due to contact with a single N individual, the probability that he will become N after n contacts is $1 - (1 - g)^{nu}$ (20). If g is small, this simplifies to fu $\left(\text{with } f = ng \text{ and } u = \frac{P_N}{P_N + P_P}\right)$ (20). Thus, the number of P individuals becoming farmers (N) per generation is

$$I = fuP_P = f\frac{P_N P_P}{P_N + P_P}. \qquad [7]$$

In systems without net reproduction (as in ref. 20, but not in our case), the population size $P_N + P_P$ is constant and the first equation of Eq. **6** becomes the well-known equation $u' = u + fu(1 - u)$ (20). We also note that for $P_N >> P_P$, the second equation of Eq. **6** becomes $P_P' = (1 - f)P_P$, which implies that $f \le 1$. We have assumed that the number n of teachers that a P individual contacts during her/his lifetime is independent of P_N and P_P. Alternatively, we could assume that n is proportional to $P_N + P_P$ (leading to the Lotka–Volterra interaction—namely, $I = kP_N P_P$). However, a constant value for n seems more realistic because the number of teachers, friends, etc. per individual is empirically observed to be roughly the same for many different populations (30). Note also that according to Eq. **7**, I becomes, e.g., independent of P_N if $P_N >> P_P$, which seems reasonable because each P individual cannot interact with an arbitrarily large number of N individuals.

More complicated models can be considered, based on the assumption that the probability g (and therefore $f = ng$) depends on $u = \frac{P_N}{P_N + P_P}$. However, the main conclusion of this paper would not change if this effect were included (*Frequency-Dependent Cultural Transmission*), so frequency-dependent models are not necessary here.

Generalized model. For our purposes, Eq. **7** has a serious limitation. If $P_N << P_P$, the first equation of Eq. **6** becomes $P_N^{'} = (1 + f)P_N$, which combined with $f \leq 1$ implies that each N individual can at most convert a single P individual in their lifetime. This result does not seem reasonable, in general, because there are many historical events where a small number of immigrants can introduce a new technology rapidly across a society. Therefore, we generalize the special case in the previous paragraph as follows. That special case assumes that a P individual is equally likely to contact with N or P individuals (so that the number of N teachers he/she contacts is $n\frac{P_N}{P_N + P_P}$). Let us now assume that, for learning purposes, a P individual contacts with only a fraction α of his/her N neighbors and a fraction β of his/her P neighbors. Then, the number of N teachers that he/she contacts is $n\frac{\alpha P_N}{\alpha P_N + \beta P_P} = n\frac{P_N}{P_N + \gamma P_P}$, where $\gamma = \frac{\beta}{\alpha}$ (the special case in the previous paragraph corresponds to $\alpha = \beta$ or $\gamma = 1$). Repeating the derivation in the previous paragraph leads to the following generalization of Eq. **7**:

$$I = f\frac{P_N P_P}{P_N + \gamma P_P}, \qquad \textbf{[8]}$$

and this yields Eq. **1**. The case $\gamma < 1$ corresponds to a higher tendency for hunter-gatherers to select farmers rather than hunter-gatherers as teachers ($\alpha > \beta$). For $P_N \ll P_P$, Eq. **8** becomes $I = CP_N$, where $C = \frac{f}{\gamma}$. Then the first equation of Eq. **6** yields $P_N^{'} = (1 + C)P_N$, which shows that C is the number of hunter-gatherers converted by each farmer per generation at the leading edge of the wave of advance ($P_N \ll P_P$). Many hunter-gatherers will be converted by each farmer if $C \gg 1$. Note that I becomes independent of P_P if $P_N \ll P_P$, I becomes independent of P_N if $P_N \gg P_P$, and both results seem reasonable (as explained below Eq. **7**).

Nonhomogeneous Systems. In this case, the population densities $N(x,y,t)$ and $P(x,y,t)$ depend on space (x,y) and time t. We discuss the evolution equation for N only, because that for P is analogous. The simplest model is called the noncohabitation model. As we shall now see, it includes Fisher's equation as a special case. The noncohabitation model (9) is based on the following assumption for the change in $N(x,y,t)$ during a generation time T (defined as the mean time interval between the migration of an individual and one of her/his children),

$$\begin{aligned} N(x,y,t+T) - N(x,y,t) = &\int_{-\infty}^{\infty}\int_{-\infty}^{\infty} N(x+\Delta_x, y+\Delta_y)\phi_N(\Delta_x,\Delta_y)d\Delta_x d\Delta_y - N(x,y,t) \\ &+ R_T[N(x,y,t)] - N(x,y,t) + f\frac{N(x,y,t)P(x,y,t)}{N(x,y,t)+\gamma P(x,y,t)}\cdot \end{aligned} \qquad \textbf{[9]}$$

In Eq. **9**, the two first terms in the right-hand side are due to population movement (dispersal), the third and fourth ones are due to net reproduction (births minus deaths), and we have added the last term to include cultural transmission, in agreement with Eq. **1** (9). Models with a distribution of generation times T yield similar results (21). The dispersal kernel $\phi_N(\Delta_x, \Delta_y)$ in Eq. **9** is the probability of migration from an area centered at $(x+\Delta_x, y+\Delta_y)$ at time t to an area centered at (x,y) at time $t+T$. The third term in the right-hand side of Eq. **9** corresponds to logistic dynamics,

$$\begin{cases} R_T[N(x,y,t)] = \dfrac{e^{a_N T}K_N\,N(x,y,t)}{K_N + (e^{a_N T}-1)N(x,y,t)} \\ R_T[P(x,y,t)] = \dfrac{e^{a_P T}K_P\,P(x,y,t)}{K_P + (e^{a_P T}-1)P(x,y,t)} \end{cases}, \qquad \textbf{[10]}$$

which agrees with many population data for humans (ref. 9 and citations therein). Assuming isotropic kernels and performing a Taylor expansion up to second order in Δ_x and Δ_y and up to first order in T yields Fisher's equation (9) with an additional term (due to cultural transmission),

$$\frac{\partial N}{\partial t} = D_N\nabla^2 N + F(N) + \frac{f}{T}\frac{NP}{N+\gamma P} \qquad \textbf{[11]}$$

where $D_N \equiv \int_{-\infty}^{\infty}\int_{-\infty}^{\infty}(\Delta_x^2 + \Delta_y^2)\phi_N(\Delta_x,\Delta_y)d\Delta_x d\Delta_y$ is the diffusion coefficient of the Neolithic population and $F(N) = a_N N\left(1 - \frac{N}{K_N}\right)$ its logistic growth function [second-order terms in T are sometimes also included (9), but they are not necessary for our purposes here]. This step completes the derivation of the reaction-diffusion Eq. **2**. However, when applied to human populations, reaction-diffusion equations can lead to substantial errors for two reasons: (*i*) It has been shown that the diffusive approximation (i.e., the second-order spatial Taylor expansion above) breaks down for realistic human dispersal kernels (11). (*ii*) According to Eq. **9**, newborn individuals can appear at (*x,y*) (terms $R_T[N(x,y,t)] - N(x,y,t)$) while their parents migrate away from (*x,y*) (first two terms in the right-hand side). In other words, some parents leave their newborn children alone. Because newborn humans cannot survive alone, it is more realistic to replace Eq. **9** by the so-called cohabitation equation (figure 1 in ref. 11, and refs. 10 and 23)—namely,

$$N(x,y,t+T) = \int_{-\infty}^{\infty}\int_{-\infty}^{\infty}\tilde{N}(x+\Delta_x, y+\Delta_y, t)\phi_N(\Delta_x,\Delta_y)d\Delta_x d\Delta_y, \qquad \textbf{[12]}$$

where

$$\tilde{N}(x,y,t) \equiv R_T[N(x,y,t)] + f\frac{R_T[N(x,y,t)]R_T[P(x,y,t)]}{R_T[N(x,y,t)] + \gamma R_T[P(x,y,t)]}. \qquad \textbf{[13]}$$

This procedure leads to Eqs. **3** and **4**, thereby generalizing the cohabitation model (23) to include cultural transmission. We have assumed that reproduction is followed by cultural transmission (Eq. **13**) and then by dispersal (Eq. **12**). However, it is easy to see that the front speed (derived below) is the same regardless of order of events. For more detailed derivations and discussions on the order of events and the basic cohabitation Eqs. **12** and **13** (without the last term in Eq. **13**), see especially figure 1 of ref. 11, figure 17 of ref. 10, and ref. 23.

Front Speed. To model the Neolithic transition, we consider farmers initially only in a given region (an area located in the Near East, according to archaeological evidence). Because humans disperse and reproduce, farmers can gradually spread into other regions (e.g., into Europe, which was initially occupied by hunter-gatherers but not by farmers, again according to archaeological evidence). In the leading edge of the advancing agricultural population front, we may linearize the population densities as

$$\begin{cases} N(x,y,t) = \varepsilon(x,y,t) + O(2) \\ P(x,y,t) = K_P - \delta(x,y,t) + O(2), \end{cases} \qquad \textbf{[14]}$$

where $\varepsilon(x,y,t) \ll K_N$, $\delta(x,y,t) \ll K_P$, and $O(2)$ are second-order terms. Then Eq. **10** becomes

$$\begin{cases} R_T[N(x,y,t)] = e^{a_N T}\varepsilon(x,y,t) + O(2) \\ R_T[P(x,y,t)] = K_P - \dfrac{\delta(x,y,t)}{e^{a_P T}} + O(2). \end{cases} \qquad \textbf{[15]}$$

Using Eq. **15** into **13** and performing a two-variable Taylor expansion yields

$$\tilde{N}(x,y,t) = e^{a_N T}(1+C)N(x,y,t) + O(2), \qquad \textbf{[16]}$$

where $C = \frac{f}{\gamma}$, and finally Eq. **12** becomes simply

$$N(x,y,t+T) \approx e^{a_N T}(1+C)\int_{-\infty}^{\infty}\int_{-\infty}^{\infty} N(x+\Delta_x, y+\Delta_y, t)\phi_N(\Delta_x,\Delta_y)d\Delta_x d\Delta_y. \qquad \textbf{[17]}$$

When observed dispersal data are used, the kernel per unit length $\varphi_N(\Delta)$ is defined as the probability to disperse into a ring of radius Δ and width $d\Delta$, divided by $d\Delta$. If individuals of the population N have probabilities p_j to disperse at distances r_j (j = 1, 2, . . ., M),

$$\varphi_N(\Delta) = \sum_{j=1}^{M} p_j \delta^{(1)}(r_j), \qquad \textbf{[18]}$$

where $\delta^{(1)}(r_j)$ is the one-dimensional Dirac δ centered at r_j (i.e., a function that vanishes everywhere except at $\Delta = r_j$). Because the total probability must be 1,

$$1 = \int_{0}^{\infty}\varphi_N(\Delta)d\Delta, \qquad \textbf{[19]}$$

and $\varphi_N(\Delta)$ is clearly a probability per unit length. In contrast, the kernel $\phi_N(\Delta_x, \Delta_y)$ in Eq. **17** is a probability per unit area (because it is multiplied by $d\Delta_x d\Delta_y$, which has units of area). The normalization condition for $\phi_N(\Delta_x,\Delta_y)$ is therefore

$$1=\int_{-\infty}^{\infty}\int_{-\infty}^{\infty}\phi_N(\Delta_x,\Delta_y)d\Delta_x d\Delta_y=2\pi\int_{0}^{\infty}\phi_N(\Delta)\Delta d\Delta, \qquad \textbf{[20]}$$

where we have used polar coordinates $\Delta=\sqrt{\Delta_x^2+\Delta_y^2}$, $\theta=\tan^{-1}(\Delta_x/\Delta_y)$, and assumed the kernel is isotropic, $\phi_N(\Delta_x,\Delta_y)=\phi_N(\Delta)$. Comparing Eqs. **19** and **20**, we see that the dispersal probability per unit length [i.e., into a ring of area $2\pi\Delta\, d\Delta$) $\varphi_N(\Delta)$ is related to that per unit area $\phi_N(\Delta)$, as in Fort and Pujol (10)],

$$\varphi_N(\Delta)=2\pi\Delta\,\phi_N(\Delta), \qquad \textbf{[21]}$$

and Eq. **18** yields

$$\phi_N(\Delta)=\sum_{j=1}^{M}p_j\frac{\delta^{(1)}(r_j)}{2\pi\Delta}. \qquad \textbf{[22]}$$

For homogeneous parameter values, the speed will not depend on direction and can thus be more easily computed along the x-axis ($y=0$). Consider a coordinate frame $z=x-st$ moving with the wave of advance (s is the wave speed). The population density of farmers will be equal to its saturation density K_N in regions where the Neolithic transition is over, and it will decay to zero in regions where few farmers have arrived ($N<<K_N$). Thus, we assume as usual the ansatz $N(x,y,t)=N_0\exp[-\lambda z]$ for $z\to\infty$ (with $\lambda>0$)(10). Then Eq. **17** becomes

$$e^{\lambda sT}=e^{a_N T}(1+C)\int_{0}^{2\pi}d\theta\int_{0}^{\infty}e^{-\lambda\Delta\cos\theta}\phi_N(\Delta)\Delta d\Delta, \qquad \textbf{[23]}$$

where we have applied that $\Delta_x=\Delta\cos\theta$. Finally, using Eq. **22** and assuming that the minimum speed is that of the front, we reach Eq. **5** for the front speed s. Numerical simulations of Eqs. **3** and **4** confirm the validity of Eq. **5** (symbols vs. curves in Fig. 1). Details on the numerical simulations can be found in *Numerical Simulations*, where it is also shown that the width of the Neolithic front (as obtained from the simulations) agrees reasonably well with the available archaeological observations.

ACKNOWLEDGMENTS. Jean-Pierre Bocquet-Appel, Marcus Feldman, Thomas N. Headland, and Neus Isern are acknowledged for providing useful information. This work was supported in part by Ministry of Science Grants SimulPast-CSD-2010-00034 and FIS-2009-13050 and the Generalitat de Catalunya Grup Consolidat 2009-SGR-374.

1. Ammerman AJ, Biagi P, eds (2003) *The Widening Harvest. The Neolithic Transition in Europe: Looking Back, Looking Forward* (Archaeol Inst Am, Boston).
2. Pinhasi R, Fort J, Ammerman AJ (2005) Tracing the origin and spread of agriculture in Europe. *PLoS Biol* 3(12):e410.
3. Fort J, Pujol T, Vander Linden M (2012) Modeling the Neolithic transition in the Near East and Europe. *Am Antiq* 77(2):203–220.
4. Ammerman AJ, Cavalli-Sforza LL (1984) *The Neolithic Transition and the Genetics of Populations in Europe* (Princeton Univ Press, Princeton).
5. Childe VG (1925) *The Dawn of European Civilization* (Kegan Paul, London).
6. Edmonson MS (1961) Neolithic diffusion rates. *Curr Anthropol* 2(2):71–102.
7. Zeder MA (2008) Domestication and early agriculture in the Mediterranean Basin: Origins, diffusion, and impact. *Proc Natl Acad Sci USA* 105(33):11597–11604.
8. Ammerman AJ, Cavalli-Sforza LL (1973) A population model for the diffusion of early farming in Europe. *The Explanation of Culture Change*, ed Renfrew C (Duckworth, London), pp 345–357.
9. Fort J, Méndez V (1999) Time-delayed theory of the Neolithic transition in Europe. *Phys Rev Lett* 82(4):867–870.
10. Fort J, Pujol T (2008) Progress in front propagation research. *Rep Prog Phys* 71(8): 086001.
11. Isern N, Fort J, Pérez-Losada J (2008) Realistic dispersion kernels applied to cohabitation reaction-dispersion equations. *J Stat Mech* 2008(10):P10012.
12. Patterson MA, Sarson GR, Sarson HC, Shukurov A (2010) Modeling the Neolithic transition in a heterogeneous environment. *J Arch Sci* 37(11):2929–2937.
13. Hamilton MJ, Buchanan B (2007) Spatial gradients in Clovis-age radiocarbon dates across North America suggest rapid colonization from the north. *Proc Natl Acad Sci USA* 104(40):15625–15630.
14. Vlad MO, Ross J (2002) Systematic derivation of reaction-diffusion equations with distributed delays and relations to fractional reaction-diffusion equations and hyperbolic transport equations: Application to the theory of Neolithic transition. *Phys Rev E Stat Nonlin Soft Matter Phys* 66(6 Pt 1):061908.
15. Fedotov S, Moss D, Campos D (2008) Stochastic model for population migration and the growth of human settlements during the Neolithic transition. *Phys Rev E Stat Nonlin Soft Matter Phys* 78(2 Pt 2):026107.
16. Ackland GJ, Signitzer M, Stratford K, Cohen MH (2007) Cultural hitchhiking on the wave of advance of beneficial technologies. *Proc Natl Acad Sci USA* 104(21): 8714–8719.
17. Gamba C, et al. (2012) Ancient DNA from an Early Neolithic Iberian population supports a pioneer colonization by first farmers. *Mol Ecol* 21(1):45–56.
18. Skoglund P, et al. (2012) Origins and genetic legacy of Neolithic farmers and hunter-gatherers in Europe. *Science* 336(6080):466–469.
19. Fort J, Méndez V (2002) Wavefronts in time-delayed systems. Theory and comparison to experiment. *Rep Prog Phys* 65(6):895–954.
20. Cavalli-Sforza LL, Feldman MW (1981) *Cultural Transmission and Evolution: A Quantitative Approach* (Princeton Univ Press, Princeton, NJ).
21. Fort J, Jana D, Humet JM (2004) Multidelayed random walks: Theory and application to the neolithic transition in Europe. *Phys Rev E Stat Nonlin Soft Matter Phys* 70(3 Pt 1):031913.
22. Fort J, Pujol T, Cavalli-Sforza LL (2004) Palaeolithic populations and waves of advance. *Camb Archaeol J* 14(1):53–61.
23. Fort J, Pérez-Losada J, Isern N (2007) Fronts from integrodifference equations and persistence effects on the Neolithic transition. *Phys Rev E Stat Nonlin Soft Matter Phys* 76(3 Pt 1):031913.
24. Newman JL (1970) *The Ecological Basis for Subsistence Change Among the Sandawe of Tanzania* (Natl Acad Sci, Washington, DC).
25. Hill K, Hurtado AM (1996) *Ache Life History* (de Gruyter, New York).
26. Bocquet-Appel JP, Naji S, Vander Linden M, Kozlowski J (2012) Understanding the rates of expansion of the farming system in Europe. *J Arch Sci* 39(2):531–546.
27. Shennan S, Edinborough K (2007) Prehistoric population history: From the late glacial to the late Neolithic in central and northern Europe. *J Arch Sci* 34(8):1339–1345.
28. Fort J (2003) Population expansion in the western Pacific (Austronesia): A wave of advance model. *Antiquity* 77(297):520–530.
29. Dickau R, Ranere AJ, Cooke RG (2007) Starch grain evidence for the preceramic dispersals of maize and root crops into tropical dry and humid forests of Panama. *Proc Natl Acad Sci USA* 104(9):3651–3656.
30. Dunbar RIM (1993) Co-evolution of neocortical size, group size and language in humans. *Behav Brain Sci* 16(4):681–735.