Front propagation and cultural transmission. Theory and application to Neolithic transitions

Joaquim Fort

Complex Systems Laboratory, Department of Physics, University of Girona, C/. Ma Aurèlia Capmany 61, 17003 Girona, Catalonia, Spain

ARTICLE INFO

ABSTRACT

We study the front propagation of a population that incorporates individuals of a second, pre-existing population. Previous models of such incorporation deal only with vertical cultural transmission (interbreeding) and horizontal cultural transmission (acculturation of individuals of the second population by members of the first one and of similar age). Here we present the first model of oblique transmission (acculturation by individuals of an older generation), which is more complicated because a model with age structure is necessary. We compare the new, age-structured model for oblique, horizontal and vertical transmission. The most powerful mechanism (fastest fronts) is oblique transmission. Two illustrative applications of Neolithic front propagation are presented. In one of them, the front was so fast that neither horizontal nor vertical transmission can explain it (but oblique transmission can). In the cases for which cultural transmission is a viable explanation, the observed front speed yields bounds on the intensity of cultural transmission. Our models are also of interest in many other Neolithic and non-Neolithic human range expansions, including major human migrations. Additionally, in future work the new age-structured models reported in this paper could be applied to model genetic gradients and, possibly, to similar phenomena in other species in which cultural transmission is well-known to occur.

1. Introduction

The propagation of reaction-diffusion fronts has been widely studied, both theoretically [1–3] and in many physical and interdisciplinary applications [3,4] such as cancer tumors [5,6], virus infections [7,8], the spread of genetic mutations [9,10] and human range expansions [11,12]. In the later application, some works have considered a single population [13–15] and others have dealt with several interacting human populations [16–18].

The first front propagation models of human range expansions [9,13,19] can be derived from the following equation for the population density (number of individuals per unit area) $p(x, y, t)$ at position (x, y) and time t [20],

$$p(x, y, t + T) - p(x, y, t) = R_T[p(x, y, t)] - p(x, y, t)$$
$$+ \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \phi(\Delta_x, \Delta_y) p(x + \Delta_x, y + \Delta_y, t) d\Delta_x \, d\Delta_y - \ p(x, y, t),$$

$$(1)$$

where the first two terms on the right-hand side give the change in population density during the time interval T due to net reproduction (births and deaths). The two last terms describe dispersal,

i.e., individuals arriving to and leaving from a unit area centered at (x, y), respectively [20]. The time interval T is the generation time, defined as the mean age difference between a parent and her/his children[1]. The dispersal kernel $\phi(\Delta_x, \Delta_y)$ is the probability per unit area than an individual who is at position $(x + \Delta_x, y + \Delta_y)$ at time t moves to (x, y) at time $t + T$, and its normalization condition is $\int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \phi(\Delta_x, \Delta_y) d\Delta_x \, d\Delta_y = 1$.

A well-known approximation, due to Fisher [9] and Kolmogorov et al. [21], can be derived by performing a first-order Taylor expansion in time and a second-order Taylor expansion in space in Eq. (1), assuming an isotropic kernel, and requiring the resulting equation without dispersal to agree with the so-called logistic equation, i.e., $\frac{\partial p}{\partial t} = ap(1 - \frac{p}{p_{max}})$, where a is called the initial growth rate and p_{max} the carrying capacity. Logistic dynamics is well-known to describe adequately net reproduction for many biological systems [22]. This procedure yields the Fisher-KPP equation, namely [9,21,20]

$$\frac{\partial p}{\partial t} = ap\left(1 - \frac{p}{p_{max}}\right) + D\left(\frac{\partial^2 p}{\partial x^2} + \frac{\partial^2 p}{\partial y^2}\right),$$

$$(2)$$

---

[1] The generation time has been estimated as $T = 32$ yr for pre-industrial populations using ethnographic data [28].

where we have replaced $p(x, y, t)$ by p for notational simplicity and $D = \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \phi(\Delta_x, \Delta_y)\Delta^2 \, d\Delta_x \, d\Delta_y$ is the diffusion coefficient, with $\Delta^2 = \Delta_x^2 + \Delta_y^2$. However, it has been shown that the diffusion approximation is not valid for human displacements [23] and it leads to substantial errors when computing Neolithic spread rates [24], so equations involving a diffusion coefficient (such as Eq. (2)) are not appropriate and a kernel $\phi(\Delta_x, \Delta_y)$ should be used instead (as in Eq. (1)) for humans.

The solution of the logistic equation introduced above Eq. (2) is [25]

$$R_T[p(x, y, t)] = \frac{p(x, y, t) \, p_{max} \, e^{aT}}{p_{max} \, + \, p(x, y, t)\left(e^{aT} - 1\right)}. \tag{3}$$

This function agrees with many data [22] and can thus be used in Eq. (1).

Eq. (1) is more general and complicated to handle than the Fisher-KPP Eq. (2). However, even Eq. (1) has a serious limitation. In a situation in which all individuals are at time t in a single location (x, y), and all of them disperse, at this location and time the third term on the right-hand side of Eq. (1) vanishes and Eq. (1) predicts that parents will move away (last term) and leave their children (first two terms on the right) at the original location. It has been shown that for this reason, Eq. (3) must be replaced by the so-called cohabitation equation, namely [26,4,27]

$$p(x, y, t + T) = R_T\left[\int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \phi(\Delta_x, \Delta_y) \, p(x + \Delta_x, y + \Delta_y, t) \, d\Delta_x \, d\Delta_y\right], \tag{4}$$

so that each individual first disperses with probability kernel $\phi(\Delta_x, \Delta_y)$ and then reproduces according to Eq. (3) (leading to new individuals the next generation[2]). Alternatively we could consider that individuals first reproduce and then disperse, or even that they reproduce during dispersal, but the front speed would be the same for all three cases (see Fig. 17 and Eqs. (172)-(176) in Ref. [4]). Models with several possible values of T are substantially more complicated but yield essentially the same results [28].

All equations above belong to the so-called demic case, i.e., that in which a front (also called wave of advance) of a population spreads due only to dispersal and reproduction, but not via cultural transmission (i.e., by incorporation of individuals from another population). Several authors have called to develop a "second generation of wave-of-advance models" that include cultural transmission in addition to demic diffusion [29,30]. Some general ideas on such models were already advanced by Ammerman and Cavalli-Sforza (pp. 116–199 in Ref. [19]). These ideas have led to interesting simulations [19,31–33] but they have been formalized to derive equations for the front speed (also called spread rate) of population waves of advance only in a few papers [27,34]. The present work aims to develop demic-cultural front propagation models by carefully taking into account the different possible mechanisms of cultural transmission.

If cultural transmission is present, one population increases due to its interaction with a second population. Our approach is valid for any cultural trait (for example, political, religious, leisure or other traits [35]). However, for clarity we will discuss our model

for the specific application that we want to consider in this work, namely the propagation of Neolithic fronts. Genetic analyses of ancient individuals [36] have shown that farmers (i.e., Neolithic individuals with number density $p(x, y, t)$) dispersed from a localized region (e.g., the Near East) over wide landscapes (e.g., Europe) that were already populated by hunter-gatherers (i.e., Mesolithic individuals with number density $q(x, y, t)$). In this application, cultural transmission is defined as the incorporation of some of these hunter-gatherers (HGs) into the expanding populations of farmers. Therefore, the population of farmers increases and that of HGs decreases. In order to model this scenario mathematically, it is necessary to take into account that cultural transmission can be of three different kinds [37], which we describe in turn. In the rest of this section we consider homogeneous systems (so that there is no dispersal) without net reproduction for simplicity. Non-homogeneous systems (i.e., population dispersal) with reproduction will be analyzed in the next sections.

(i) Vertical cultural transmission. In this case, there is an increase in the number of farmers due to the fact that some of them mate with HGs. It is well-known from ethnographic observations that the children of such cross-matings are always farmers, not HGs (see, e.g., pp. 111 and 409 in Ref. [38] and p. 170 in Ref. [30]). The equations that describe this process have been derived using vertical transmission theory [37]. As mentioned above, in the rest of this introduction we consider the case in which there is no net reproduction (e.g., all indiviauals mate and each couple has on average two surviving children). Then the population densities evolve according to (see Eqs. (14), (39) and (42) in Ref. [34])

$$\begin{cases} p' = p + \eta \frac{p \, q}{p+q} \\ q' = q - \eta \frac{p \, q}{p+q}, \end{cases} \tag{5}$$

where p is the number density of the population (farmers in our application) that incorporates members of the second population (HGs in our case), which has number density q. Number densities without primes are those before cultural transmission, whereas primes denote the corresponding values after cultural transmission (in vertical transmission or interbreeding, this is equivalent to before and after reproduction). The parameter η is called the intensity of vertical cultural transmission. Note that $\eta \geq 0$ because negative values of η would lead to a decrease in the number density of farmers p, in disagreement with the ethnographic observations cited above Eqs. (5). If $p \gg q$ the second equation reads $q' = q(1 - \eta)$, so values $\eta > 1$ would imply $q' < 0$. Thus range of possible values for η is $0 \leq \eta \leq 1$. Also if $p \gg q$, for $\eta = 1$ Eqs. (5) yield $p' = p + q$ and $q' = 0$, so HGs disappear because all of them mate with farmers [34]. In the opposite limit ($q \gg p$), the first equation yields $p' = p(1 + \eta)$, so the bound $\eta \leq 1$ implies that $p' \leq 2p$, which is reasonable because each farmer is assumed to mate with a single person in this model [34], so the number of HGs (ηp) incorporated per unit area is at most (for $\eta = 1$) equal to the initial number of farmers (p).

(ii) Horizontal cultural transmission. In this case, members of one population leave it and become members of the other, due to their interactions with individuals of the same generation but belonging to the other population. For example, in our application the increase in the number of farmers under horizontal transmission is due to the fact that some HGs convert into farmers by gaining access to domesticated plants and/or animals and learning agricultural techniques from farmers of the same generation. The equations that describe this process have been derived previously [27] and are as follows

$$\begin{cases} p' = p + f \frac{p \, q}{p + \gamma \, q} \\ q' = q - f \frac{p \, q}{p + \gamma \, q}, \end{cases} \tag{6}$$

---

[2] A time interval $T = 32$ later on average, as mentioned in footnote [1].

where f and γ are positive parameters of horizontal transmission. There is no cultural transmission if $f = 0$. As above, the population densities without and with primes denote before and after cultural transmission, but the time interval elapsed between them is arbitrary for horizontal transmission because no interbreeding is necessary (in contrast to the case of vertical transmission discussed above). As mentioned above, in horizontal transmission HGs learn agriculture from farmers and become farmers themselves, so $p' \geq p$ and therefore $f \geq 0$ (the reverse transition, i.e., farmers becoming HGs, is very rarely observed [39]). The second parameter, γ, is a measure of the preference by HGs to select farmers rather than HGs (if $\gamma < 1$) or HGs rather than farmers (if $\gamma > 1$) as teachers [27]. The range of possible values of parameter f is $0 \leq f \leq 1$ because if $p \gg q$, values $f > 1$ would imply $q' < 0$ according to the second equation. In the opposite limit ($q \gg p$), the first equation yields $p' = (1 + \frac{f}{\gamma}) p$, so although $f \leq 1$ there is no limit in principle to the number of HGs ($\frac{f}{\gamma} p$) that become farmers, in contrast to what we have seen for vertical transmission (the reason is that the vertical case corresponds to interbreeding, for which there is a limit equal to the initial number of HGs if each farmer mates with a single person [34]; in contrast for horizontal transmission a farmer can in principle teach agriculture to an arbitrarily large number of HGs [27]). It is possible to generalize this model in order to include frequency-dependent cultural transmission (see Eq. [S3] in Ref. [27]) but the equations would be substantially more complicated and lead to the same conclusions, so we will not consider them in the present paper.

Eqs. (6) are more appropriate for our purposes than, e.g., the Lotka-Volterra interaction (often used in predator-prey and competition ecological systems) for the following two reasons. First, in contrast to Lotka-Volterra equations, Eqs. (6) were derived [27] using cultural transmission theory [37]. Second, the Lotka-Volterra interaction assumes that the number of teachers that an individual contacts during her/his lifetime is proportional to the population density, whereas ethnographic data indicate that this number is essentially independent of the population density [27].

(iii) Oblique cultural transmission. In this type, adult individuals teach members of the next generation, i.e., younger individuals. A very clear example is the schooling system in modern populations, but oblique transmission is also observed in preindustrial populations [40]. The derivation [27] of Eqs. (6) remains valid, but we have to distinguish adult individuals (teachers) from younger ones (learners). For the applications that we want to consider in this paper (Neolithic fronts), we have to consider the case in which adult individuals of the Neolithic population (adult teachers with population density p_A) teach farming to young individuals of the hunter-gatherer population (infantile learners with population density q_I). Thus we can use Eqs. (6) but distinguishing adult from infantile individuals,

$$\begin{cases} p_A' = p_A + g\frac{p_A \, q_I}{p_A + \delta \, q_I} \\ q_A' = q_A - g\frac{p_A \, q_I}{p_A + \delta \, q_I}, \end{cases} \tag{7}$$

where g and δ are positive parameters of oblique transmission. If $p_A \gg q_I$ the second equation yields $q_A' = q_A - gq_I$, so there is not any bound in principle on g (in contrast to those for η and f following from Eqs. (5) and (6), respectively). According to the first of Eqs. (7), the number density of adults of the first population (p_A) increases after some children of the second population (q_I) have converted into members of the first population and grown into adults (p_A). In the last equation the number density of adults of the second population (q_A) is therefore smaller by the same amount, relative to the case in which no children are converted (i.e., vanishing oblique cultural transmission, $g = 0$).

There is no theory on front propagation under the *oblique* mode of transmission, only for the vertical [34] and horizontal [27] ones.

One reason may be that oblique transmission is inherently more difficult to model using equations (see the next section). The main purpose of this paper is precisely to develop a theory of front propagation under *oblique* cultural transmission. We will also compare the results to those for *vertical* and *horizontal* transmission, as well as to empirical data for two specific case studies. But first we need to develop a realistic age-dependent model without cultural transmission (Section 2).

2. Age-structured model

Since for *oblique* transmission young members of the population learn from older ones, we obviously need to distinguish among both age groups (in contrast to Eqs. (5) and (6), which hold for *vertical* and *horizontal* transmission respectively). We will thus consider two sub-populations, which are enough for our purposes and very convenient in order to add oblique cultural transmission in the next section (which will complicate the mathematical framework). Therefore, we divide the population of farmers $p(x, y, t)$ into infantile and adult subpopulations, with number densities $p_I(x, y, t)$ and $p_A(x, y, t)$ respectively. We use an approach similar to those of previous age-structured models of biological invasions in one dimension [41,42] and two dimensions [43,44]. We consider the two-dimensional case, but in our equations we will take into account the special features of the application that we want to describe (cultural transmission in human populations). In this section we consider the case without cultural transmission. For our purposes, the following set of equations will be adequate,

$$\begin{cases} p_I(x, y, t + \tau) = F \, p_A(x, y, t) \\ p_A(x, y, t + \tau) = (1 - m_I) \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \phi(\Delta_x, \Delta_y) \\ p_I(x + \Delta_x, y + \Delta_y, t) d\Delta_x \, d\Delta_y + (1 - m_A) \, p_A(x, y, t), \end{cases} \tag{8}$$

where F is the fecundity, defined as the number of children born per adult during the time interval τ that are still alive at the end of this interval. Thus the first of Eqs. (8) implies that p_I is the population density of individuals with ages between 0 and τ. This implies that the adult population density p_A corresponds to individuals with ages above τ. Infantile individuals do not reproduce, and this is why no fecundity appears in the second of Eqs. (8). There is a dispersal kernel only in the first term of the second of Eqs. (8) (conversion of infantile individuals into adults) because we assume that most of the dispersal occurs only as infantile individuals become adults (see Eqs. (8)-(9b) in Ref. [41] for a one-dimensional model with this feature). This approximation is reasonable in our case because it has been observed that for most individuals of rural populations, the only relevant movement is the dispersal from the parental home to form a new family (first term in the last of Eqs. (8)) and reproduce in a new location (first of Eqs. (8)) [23], and the same behavior is observed for pre-industrial populations [45]. These simplifications seem realistic and will make it possible to add oblique transmission (Section 3) without complicating the equations substantially. In the last of Eqs. (8) m_I is the infantile mortality, defined so that a portion m_I of the individuals who are aged between 0 and τ years at time t will have died by time $t + \tau$. Similarly m_A is the adult mortality, defined so that a portion m_A of individuals with age above τ at time t will have died by time $t + \tau$. After this time interval τ, the adult population p_A is composed by individuals with ages between τ and 2τ (first term on the right-hand side of the last of Eqs. (8)) and individuals with ages above 2τ (second term). The total population density is[3]

$$p(x, y, t) = p_I(x, y, t) + p_A(x, y, t). \tag{9}$$

---

[3] We can compare the age-structured model (8) to the previous one without age structure (4) by considering for simplicity the homogeneous case (no dispersal) with $m_I = 0$. Then Eqs. (8) are simply $p_I(t + \tau) = F \, p_A(t)$ and $p_A(t + \tau) =$

Concerning the parameter values, we think that a time interval of about $\tau = 16$ yr is reasonable because reproduction begins at about age 16 in pre-industrial populations (p. 67 in Ref. [45]). Moreover, in such populations life expectancy is short and children have acquired most of their skills before the age of 16 yr via cultural transmission [40]. This also suggests that, in order to include cultural transmission between the two subpopulations (as done in the next section), our range for the infantile subpopulation p_I (0-16 yr) is realistic. Thus the adult population p_A is composed by individuals with ages above 16 years (see the paragraph above Eq. (9)).

For the dispersal kernel $\phi(\Delta_x, \Delta_y)$ in Eqs. (8) we assume for simplicity that individuals do not disperse with probability p_e (which is called the persistence in demography) and disperse a characteristic distance r with probability $(1 - p_e)$. This simple kernel has yielded Neolithic spread rates consistent with the observed ones [26,34,16]. Then

$$\phi(\Delta_x, \Delta_x) = p_e \; \delta^{(2)}(\Delta) + (1 - p_e) \; \delta^{(2)}(\Delta - r), \tag{10}$$

where $\delta^{(2)}(\Delta) = \frac{\delta^{(1)}(\Delta)}{2\pi\Delta}$ is the two-dimensional Dirac delta function centered at $\Delta = 0$ (i.e., per unit area), $\delta^{(1)}(\Delta)$ is the corresponding one-dimensional function (i.e., per unit length), and $\Delta = \sqrt{\Delta_x^2 + \Delta_y^2}$. The values $p_e = 0.38$ and $r = 50$ km have been estimated previously [26] from ethnographic data of pre-industrial populations. We stress that more complicated models are possible, but we are interested in the simplest possible one so that we can focus our attention on cultural transmission (next section).

Finally, the net fecundity appearing in the first of Eqs. (8) can be estimated as $F = 2.69$ children per adult[4], the infantile mortality appearing in the second of Eqs. (8) as $m_I = 0.29$[5], and the adult mortality in the same equation as $m_A = 0.49$[6].

$p_I(t) + (1 - m_A) \; p_A(t)$. Adding them up yields $p(t + \tau) = (F + 1 - m_A) \; p_A(t) + p_I(t)$, so $p(t + 2\tau) = (F + 1 - m_A) \; p_A(t + \tau) + p_I(t + \tau) = Fp(t) + (1 - m_A)p_I(t) + (F + 1 - m_A)(1 - m_A)p_A(t)$. This is not an equation with the form of Eq. (4) except if $m_A = 1$. In this case $p(t + 2\tau) = F \; p(t)$, which agrees with Eq. (4), namely $p(t + T) = R_T[p(t)] \approx R_0 \; p(t)$ (at the front leading edge, i.e., for small values of $p(t)$) if $R_0 = e^{aT}$, $T = 2\tau$ and $R_0 = F$. Thus the age-structured model cannot agree with the model without age structure unless $m_A = 1$, i.e., unless we neglect adults above age $T = 2\tau$. This would be realistic only if adults did not reproduce appreciably above age T. But T in Eq. (4) is the age difference between a parent and his/her children, so all individuals would produce at age T years F children at once. Obviously this approximation (and thus the model without age structure) is not realistic for humans, so we keep the last term in the second of Eqs. (8).

[4] It is well-known that human fertility is very high in the case of pre-industrial farming populations expanding in areas previously empty of farmers. Very detailed data exist for the case of French settlers in the St. Lawrence Valley (Canada) during the 17th and 18th centuries, which imply a fertility of 10.2 children per woman [76], i.e., 5.1 children per adult. These women reproduced on average during 20 years of their lives (namely, at ages 21-41 on average) [76]. Thus the number of children per adult born during 16 years is about $5.1 \bullet 16/20 = 4.08$. As noted below Eqs. (8), in our model F is this number but including only those children who are still alive at age 16 yr. Thus, we take into account that a mortality of about 33% for infantile individuals (below 16 yr) has been estimated for the same population (p. 124 in Ref. [75]), which yields for the net fecundity $F \approx 4.08 \cdot 0.66 = 2.69$ children per adult (during a period of $\tau = 16$ yr, in agreement with the first of Eqs. (7)).

[5] We have not found detailed mortality estimations for the St. Lawrence Valley population, but some archaeological data are useful for this purpose. Ref. [61] determined the ages of 262 Neolithic skeletons and reported (Table 4) the number of deaths in intervals of 10 years. Using the mean age of each interval, it is easy to perform two estimations of m_I, namely using the number of individuals alive at age 6 (and dead 16 yr later) and those alive at age 16 (and dead 16 yr later). Both results are similar and their average is $m_I = 0.29$, i.e., 29% of the infantile individuals (ages 0-16 yr) who are alive at time t will have died by time $t + 16$ yr, i.e., when they would be aged 16-32 yr (see the text below Eqs. (8)).

[6] Also from Table 4 in Ref. [61], it is easy to perform estimations of m_A using the number of individuals alive at age 26 (and dead 16 yr later) and those alive at age 36 (and dead 16 yr later). Both results are similar and their average is $m_A = 0.49$, i.e., that 49% of the adults (ages above 16 yr) who are alive at time t will have died by time $t + 16$ yr, i.e., when they would be aged above 32 yr (see the text below Eqs. (8)).

3. Cultural transmission and the spread of the Neolithic in Europe

3.1. Oblique cultural transmission

As explained in Section 1, by definition in *oblique* transmission young individuals learn from older ones (excluding their parents) [37]. For this reason, we have developed in Section 2 a model with two age groups (infantile and adult individuals). However, this is not enough because we want to develop a model that can be applied to Neolithic spread. In this case, some young members *of one population*, i.e., hunter-gatherers (HGs) or Mesolithics, learn agricultural techniques from old members *of a different* population, i.e., farmers or Neolithics, and in this way some HGs become farmers. For our purpose, obviously we need to consider the population densities of *four* sub-populations, namely those of infantile farmers $p_I(x, y, t)$, adult farmers $p_A(x, y, t)$, infantile HGs $q_I(x, y, t)$ and adult HGs $q_A(x, y, t)$. Clearly we have to deal with four coupled integro-difference equations of the kind of Eqs. (8), which under the *oblique* mode of interaction are given by (see Eqs. (7))

$$\begin{cases} p_I(x, y, t + \tau) = F \; p_A(x, y, t) \\ p_A(x, y, t + \tau) = (1 - m_I) \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \phi(\Delta_x, \Delta_y) p_I(x', y', t) d\Delta_x \, d\Delta_y \\ + (1 - m_I) \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \phi(\Delta_x, \Delta_y) g \frac{p_A(x', y', t) \; q_I(x', y', t)}{p_A(x', y', t) + \delta \; q_I(x', y', t)} d\Delta_x \, d\Delta_y \\ + (1 - m_A) \; p_A(x, y, t) \\ q_I(x, y, t + \tau) = F_q \; q_A(x, y, t) \\ q_A(x, y, t + \tau) = (1 - m_{Iq}) \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \phi_q(\Delta_x, \Delta_y) \; q_I(x', y', t) d\Delta_x \, d\Delta_y \\ - (1 - m_I) \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \phi(\Delta_x, \Delta_y) g \frac{p_A(x', y', t) \; q_I(x', y', t)}{p_A(x', y', t) + \delta \; q_I(x', y', t)} d\Delta_x \, d\Delta_y \\ + (1 - m_{Aq}) \; q_A(x, y, t). \end{cases}$$

$$\tag{11}$$

where $x' = x + \Delta_x$ and $y' = y + \Delta_y$. The second term in the second equation corresponds to the fact that infantile HGs learn many skills (including food procurement and preparation) during their childhood [40] and this term drives the dynamics of learning of agricultural techniques by infantile HGs (with ages $0 - \tau$ and population density $q_I(x, y, t)$) from adult farmers (with ages $> \tau$ and population density $p_A(x, y, t)$). In this way, some HGs are converted into farmers, leading τ years later (when the children have grown into adults) to an increase in the number of adult farmers (second equation, left). This corresponds to the same decrease (fourth equation, second term) in the number of adult HGs (compared to the case without conversion of HGs into farmers, i. e., $g = 0$). We have taken into account the effect of the infant mortality m_I of the converted farmers in both terms. In the last two of Eqs. (11) we have introduced the fertility, dispersal kernel and mortalities of HGs (F_q, $\phi_q(\Delta_x, \Delta_y)$, m_{Iq} and m_{Aq}, respectively) although below we shall show that they have no effect on the front speed.

We consider the case in which individuals of the population with number density p (farmers or Neolithics in our applications) spread over a region where they encounter a second, autochthonous population with number density q (HGs or Mesolithics in our case). In areas far behind the front there is only the first population at its saturation density p_{max}, so that the adult and infantile sub-populations of farmers are also at their saturation values ($p_A = p_{A \; max}$ and $p_I = p_{I \; max}$). In areas far ahead of the front, in contrast, the first population has not arrived yet and there is only the second population ($q_A = q_{A \; max}$ and $q_I = q_{I \; max}$). In the leading edge of the front, i.e., the region where only a few individuals of the first population have arrived, obviously $p_A \approx 0$, $p_I \approx 0$, $q_A \approx q_{A \; max}$ and $q_I \approx q_{I \; max}$, so the non-linear interaction (in the second terms of the second and fourth of Eqs. (11)) may be linearized by performing a two-variable, first-order Taylor

expansion around the values $p_A = 0$ and $q_I = q_{I\ max}$. Then

$$g \frac{p_A\ q_I}{p_A\ +\ \delta\ q_I}\ =\ C_o\ p_A + O(2), \tag{12}$$

where $O(2)$ stands for second and higher-order terms and

$$C_o = \frac{g}{\delta} \tag{13}$$

is a purely cultural parameter that we call the intensity of oblique cultural transmission, for the following reason. Let us focus for a moment on cultural transmission by leaving aside demographic and dispersal effects, i.e., considering the case without mortality ($m_I = 0$, $m_A = 0$ and $m_{Aq} = 0$) neither dispersal ($\phi(\Delta_x, \Delta_x) = \delta^{(2)}(\Delta)$). Then, when the first farmers arrive to a region $p_A \approx 0$, the increase $\Delta\ p_A$ in the adult farmer number density p_A (and the decrease $\Delta\ q_A$ in the adult HG number density q_A) due to oblique transmission (second and third terms in the second and fourth of Eqs. (11)) is given by Eqs. (7) and (12), i.e.,

$$\frac{\Delta\ p_A}{p_A} = -\frac{\Delta\ q_A}{p_A} \approx C_o \tag{14}$$

where $\Delta\ p_A = p_A' - p_A$, $\Delta\ q_A = q_A - q_A'$, and number densities without primes are those before cultural transmission, whereas primes denote the corresponding values after cultural transmission (as in Eqs. (7)). Eq. (14) implies that when the first members of the population that expands its range (e.g., farmers) arrive, C_o is the number of individuals of the autochthonous population (e.g., HGs) converted into members of the invading population (e.g., farmers) due to oblique transmission by each pioneering individual (e.g., farmer). In this sense, C_o can be called the intensity of oblique transmission.

Using Eq. (12), the leading-edge version of the two first equations in the set (11) is

$$\begin{cases} p_I(x, y, t + \tau) = F\ p_A(x, y, t) \\ p_A(x, y, t + \tau) = (1 - m_I) \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \phi(\Delta_x, \Delta_y)[p_I(x', y', t) \\ \quad + C_o\ p_A(x', y', t)]d\Delta_x\ d\Delta_y + (1 - m_A)\ p_A(x, y, t). \end{cases} \tag{15}$$

Note that neither q_I nor q_A appear in Eqs. (15), i.e., these two equations are decoupled from those for q_I and q_A (last two Eqs. of the set (11), the linearized versions of which we do not include in Eqs. (15) because we will not need them). This decoupling is not surprising because in models without age structure, the evolution equation of the invading population (p) is also decoupled from that of the autochthonous population (q), which makes calculations substantially simpler [46,26,34,27]. The difference is that here we have to deal with two Eqs. (15) to find the front speed, whereas in models without age structure we deal with only one equation [46,26,34,27], namely that for the invading population (with the population density of the autochthonous one approximated to its saturation value, analogously to our Eqs. (14) and (15)).

We assume that population p expands its range from a localized region, so the front curvature will gradually diminish (e.g., if the initial region is a circle, the ranges at later times will be circles with the same center and increasing radius). Clearly, for large enough times since the start of the dispersal the front will be approximately planar at the scale of the individual dispersal events, so we can choose the x-axis parallel to the local front propagation direction, as in previous work [46,26]. Let $s = |s_x|$ stand for the front speed ($s_y = 0$). As usual [3,4] we introduce the co-moving coordinate $z = x - st$ and look for constant-shape solutions (i.e., such that they depend only on z) of the form $p_I(x, y, t) = w_I \exp[-\lambda z]$ and $p_A(x, y, t) = w_A \exp[-\lambda z]$ with $\lambda > 0$ in the leading edge of the front ($p_A \approx 0$ and $p_I \approx 0$ or $z \to \infty$). Then Eqs. (15) reduce to the following set,

$$\begin{cases} -e^{\lambda s\tau}\ w_I + F w_A = 0 \\ (1 - m_I)\ f(\lambda r)w_I + \left[-e^{\lambda s\tau} + (1 - m_I)C_o\ f(\lambda r) + (1 - m_A)\right]w_A = 0, \end{cases} \tag{16}$$

where we have applied Eq. (10) and the text below it to perform the following integral,

$$f(\lambda r) \equiv \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} e^{-\lambda \Delta_x}\ \phi(\Delta_x, \Delta_y)\ d\Delta_x\ d\Delta_y$$

$$= \int_0^{2\pi} d\theta \int_0^{\infty} d\Delta\ e^{-\lambda \Delta\ \cos\theta}\ \frac{p_e\ \delta^{(1)}(\Delta) + (1 - p_e)\ \delta^{(1)}(\Delta - r)}{2\pi}$$

$$= p_e\ + (1 - p_e)I_0(\lambda r) \tag{17}$$

and $I_0(\lambda r) = \frac{1}{2\pi} \int_0^{\infty} d\theta\ \exp[\lambda\ r\ \cos\theta]$ is the modified Bessel function of the first kind and order zero. Introducing $\varrho = e^{\lambda s\tau}$ and using matrix notation, the set of Eqs. (16) can be written as

$$\rho \begin{pmatrix} w_I \\ w_A \end{pmatrix} = M \begin{pmatrix} w_I \\ w_A \end{pmatrix} \tag{18}$$

where the matrix M is given by

$$M = \begin{pmatrix} 0 & F \\ (1 - m_I)f(\lambda r) & (1 - m_I)\ C_o\ f(\lambda r) + (1 - m_A) \end{pmatrix} \tag{19}$$

For sufficiently steep initial conditions (e.g., if the invading population is initially at its carrying capacity in a finite region and absent outside it), it is possible to calculate the relaxation dynamics of the front towards its asymptotic shape and speed [1]. For equations of the type (15), it is well-known that the front speed converges to [41]

$$s = \frac{min}{\lambda > 0} \frac{\ln \rho_1(\lambda)}{\lambda \tau} \tag{20}$$

where $\rho_1(\lambda)$ is the largest of the eigenvalues of the linearized matrix M. As shown above, this matrix M is given by Eq. (19) for oblique cultural transmission. In this case, we can find a more explicit solution because we are dealing with only two equations (or equivalently, with a second-order matrix). For a non-trivial solution to the homogeneous set of linear Eqs. (16) to exist, the determinant of its corresponding matrix must vanish. Therefore, recalling also that $\varrho = e^{\lambda s\tau}$,

$$\begin{vmatrix} -\varrho & F \\ (1 - m_I)f(\lambda r) & -\varrho + (1 - m_I)\ C_o\ f(\lambda r) + (1 - m_A) \end{vmatrix} = 0 \tag{21}$$

This yields a second-order equation for ϱ. By solving it, we can easily find the largest solution, which is obviously the largest eigenvalue $\rho_1(\lambda)$ of the matrix (19). Using it into Eq. (20) yields the following final result for the front speed

$$s_o = \frac{min}{\lambda > 0} \frac{\ln \frac{(1-m_I)\ C_o\ f(\lambda r) + (1-m_A) + \sqrt{[(1-m_I)\ C_o\ f(\lambda r) + (1-m_A)]^2 + 4F(1-m_I)\ f(\lambda r)}}{2}}{\lambda \tau}, \tag{22}$$

where we have used the sub-index o in the left-hand side to denote oblique transmission.

In order to illustrate the applicability of the model, we use the parameter values estimated above for pre-industrial farmers ($m_A = 0.49$, $m_I = 0.29$, $= 2.69$, $p_e = 0.38$, $r = 50$ km, and $\tau = 16$ yr) into Eq. (22) to obtain the front speed as a function of the intensity of oblique cultural transmission s_o (full line in Fig. 1). This figure makes it possible to compare the front speed predicted by Eq. (22) to the observed range (hatched rectangle) for the speed of the Neolithic front in Europe. This observed range was estimated from the dates of Neolithic sites in Europe, which show that the Neolithic appeared first in the Near East and spread gradually westwards and northwards across Europe, from about 12,000 to about 5,000 years ago, with a speed in the range 0.9–1.3 km/yr [27,47] (hatched rectangle in Fig. 1). The intensity C_o of oblique transmission of agricultural techniques from pre-industrial farmers to HGs (x-axis in Fig. 1) is the only parameter in Eq. (22) that we cannot estimate independently of the front spread rate s (due
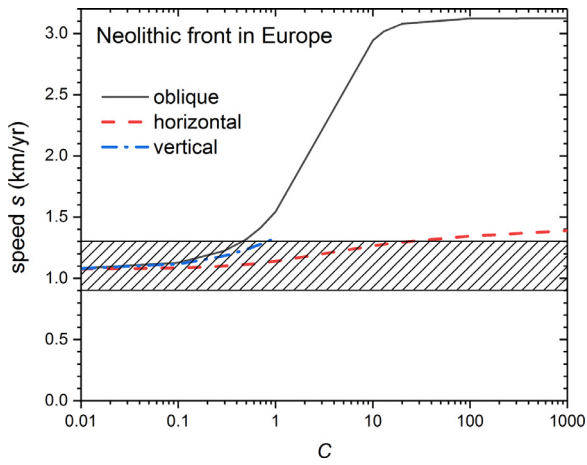
Fig. 1. Speed of the Neolithic front of farmers in Europe as a function of the intensity C of cultural transmission ($C = C_o$ for oblique, $C = C_h$ for horizontal and $C = C_v$ for vertical transmission). The x-axis scale is logarithmic to increase the visibility of the allowed range for vertical cultural transmission ($0 \leq C_v \leq 1$) as well as of the asymptotic behavior ($C \to \infty$) for oblique and horizontal transmission. For all three curves, the parameter values are $p_e = 0.38$, $r = 50$ km, $m_A = 0.49$, $m_I = 0.29$, $F = 2.69$ and $\tau = 16$ yr, as estimated in the main text for pre-industrial farmers using ethnographic and archaeological data. The hatched rectangle gives the observed front speed according to archaeological data (0.9-1.3 km/yr).

to lack of data that seem realistic for cultural transmission in the early Neolithic).

We see in Fig. 1 (black full line) that the front speed increases for increasing values of the intensity C_o of oblique cultural transmission, which is reasonable because a higher value of C_o implies a larger population of farmers (by conversion of HGs), which will in turn reproduce and disperse, therefore increasing the front spread.

According to Fig. 1, for $C_o \to \infty$ the maximum speed under oblique transmission is r/τ, i.e., 3.13 km/yr using the values above of r and τ. This asymptotic limit can be understood as the maximum dispersal distance (r for the kernel (10)) of individuals of the population that expands its range (farmers or Neolithics in our case) divided by the time interval of each interaction (τ for Eqs. (11)), i.e., r/τ. This is analogous to previously-studied cases in which there was either only a single population or two interacting populations without oblique transmission[7].

The percentage of the effect of oblique transmission on the front speed is $100(s_o - s_D)/s_D$, where s_D is the purely demic speed, i.e., that without cultural transmission (s_D can be obtained by using $C_o = 0$ into Eq. (22), which yields $s_D = 1.08$ km/yr). According to Fig. 1, the maximum possible value of this oblique effect (full curve for $C_o \to \infty$, i.e., $s_o = s_\infty = 2r/\tau$) is 190%. In other words, the speed with oblique transmission can be up to about three times faster than without cultural transmission.

For the observed range of the Neolithic front in Europe (hatched rectangle in Fig. 1), the maximum speed is $s_o = 1.3$ km (so the maximum cultural effect is 21%) and this imposes an upper bound on the intensity of oblique cultural transmission, namely $C_o < 0.5$ (Fig. 1, intersection between the full curve and the upper side of the hatched rectangle). According to Eq. (14) this implies that, at most, about 50% of adult farmers converted a HG into a farmer (by providing domesticates and teaching agricultural techniques to him/her). We believe that this is a clear illustration of how the analysis of front propagation can serve to understand some aspects of human behavior quantitatively.

---

7 See, e.g., the values of s^* in Ref. [27], Fig. 1 for the latter case.

3.2. Horizontal cultural transmission

Although the main aim of this work is to model the propagation of demic-cultural fronts under oblique cultural transmission (previous subsection), it will be also interesting to compare to horizontal and vertical transmission. In this way, we will improve (by adding age structure) previous models of front propagation under horizontal [27] and vertical [34] transmission. In this subsection we consider horizontal transmission.

As explained in Section 1, by definition in horizontal transmission teachers and learners are members of the same generation. It is not reasonable to believe that infantile farmers (aged 0-16 years) already know the agricultural techniques. Instead, it is adult farmers who can teach agriculture (as in the previous case). This implies that, in *horizontal* transmission, the learners are *adult* HGs. These convert into farmers. Thus taking into account Eqs. (6), the evolution equations are for the horizontal case

$$\begin{cases} p_I(x, y, t + \tau) = F \; p_A(x, y, t) \\ p_A(x, y, t + \tau) = (1 - m_I) \; \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \phi(\Delta_x, \Delta_y) p_I(x', y', t) d\Delta_x \; d\Delta_y \\ \quad + (1 - m_A) \; p_A(x, y, t) + (1 - m_A) f \frac{p_A(x,y,t) \; q_A(x,y,t)}{p_A(x,y,t) + \; \gamma \; q_A(x,y,t)} \\ q_I(x, y, t + \tau) = F_q \; q_A(x, y, t) \\ q_A(x, y, t + \tau) = \left(1 - m_{Iq}\right) \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \phi_q(\Delta_x, \Delta_y) \; q_I(x', y', t) d\Delta_x d\Delta_y \\ \quad + \left(1 - m_{Aq}\right) q_A(x, y, t) - (1 - m_A) f \frac{p_A(x,y,t) \; q_A(x,y,t)}{p_A(x,y,t) + \; \gamma \; q_A(x,y,t)}. \end{cases} \tag{23}$$

The second and fourth equations were applied in Ref. [27] (Eqs. [3]-[4]) to the complete populations (i.e., using $p(x, y, t)$ instead of $p_A(x, y, t)$ and $q(x, y, t)$ instead of $q_A(x, y, t)$, zero mortalities and omitting the first term on the right). However Eqs. (23) are more accurate because, as we have explained (footnote [3]), the age-structured model developed in this paper (Section 2) is more realistic for humans than the model without age structure applied in Ref. [27].

Repeating the same steps as in the previous subsection, we find that Eqs. (12)-(13) are replaced by

$$f \frac{p_A \; q_A}{p_A + \gamma q_A} = \; C_h \; p_A + O(2), \tag{24}$$

where

$$C_h = \frac{f}{\gamma} \tag{25}$$

is the intensity of horizontal cultural transmission. The oblique Eqs. (14)-(16), (19) and (21) are respectively replaced by

$$\frac{\Delta \; p_A}{p_A} = -\frac{\Delta \; q_A}{p_A} \approx C_h, \tag{26}$$

$$\begin{cases} p_I(x, y, t + \tau) = F \; p_A(x, y, t) \\ p_A(x, y, t + \tau) = (1 - m_I) \; \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \phi(\Delta_x, \Delta_y) p_I(x', y', t) d\Delta_x \; d\Delta_y \\ \quad + (1 - m_A)(1 + C_h) p_A(x, y, t), \end{cases} \tag{27}$$

$$\begin{cases} - e^{\lambda s \tau} \; w_I + F w_A = 0 \\ (1 - m_I) \; [p_e \; + (1 - p_e \;) I_0(\lambda r)] w_I + \left[- e^{\lambda s \tau} + (1 - m_A)(1 + C_h) \right] w_A = 0, \end{cases} \tag{28}$$

$$M = \begin{pmatrix} 0 & F \\ (1 - m_I)[p_e \; + (1 - p_e \;) I_0(\lambda r)] & (1 - m_A)(1 + C_h) \end{pmatrix}, \tag{29}$$

$$\begin{vmatrix} -\varrho & F \\ (1 - m_I)[p_e \; + (1 - p_e \;) I_0(\lambda r)] & -\varrho + (1 - m_A)(1 + C_h) \end{vmatrix} = 0. \tag{30}$$

and the front speed under horizontal cultural transmission is

$$s_h = \frac{min}{\lambda > 0} \frac{\ln \frac{(1-m_A)(1+C_h) + \sqrt{(1-m_A)^2(1+C_h)^2 + 4(1-m_I)F \; [p_e \; + (1-p_e \;) I_0(\lambda r)]}}{2}}{\lambda \tau}, \tag{31}$$

where s_h denotes the front speed in the presence of horizontal cultural transmission. In Fig. 1 (red dashed line) we see that the speed increases very slowly under horizontal transmission (dashed line) compared to the previous case of oblique transmission (full line). This can be understood by considering, again, the maximum possible speed. For the horizontal case ($C_h \to \infty$) it is given by $s_\infty = r/(2\tau) = 1.56$ km/yr. This value is not reached for the dashed line in Fig. 1 because the front speed increases very slowly (even for $C_h = 10,000$, the speed is only 1.42 km/yr). In contrast, in the oblique case the maximum speed ($C_o \to \infty$) is twice faster, namely r/τ (see the text 4 paragraphs below Eq. (22)). Mathematically, this difference is due to the fact that there is only one integral of the dispersal kernel in the horizontal Eqs. (27) of the invading population (farmers), whereas two kernels appear in the oblique Eqs. (15), one for infantile farmers (p_I) and another one for adult farmers (p_A). For this reason, the maximum horizontal front speed ($r/(2\tau)$) is only half than the oblique one (r/τ) and the maximum horizontal effect, $100(s_\infty - s_D)/s_D = 45\%$, is also substantially smaller than that found in the previous subsection for oblique transmission (190%). Thus oblique transmission is much more powerful than horizontal transmission, in the sense that it can yield substantially faster fronts. An intuitive explanation of this difference is that in the oblique mode [Eqs. (11)] infantile HGs are converted into farmers and disperse (thereby propagating the Neolithic front), whereas in the horizontal mode [Eqs. (22)] it is adult HGs who are converted (not infantile individuals), so they have already dispersed (or, equivalently, some time will pass before they reproduce, their children grow into adults and disperse).

As noted at the end of the previous subsection, for the observed range of the Neolithic front in Europe (hatched rectangle in Fig. 1) the maximum speed is $s_o = 1.3$ km (so the maximum cultural effect is 21%) and this imposes an upper bound on the intensity of oblique cultural transmission. For horizontal transmission this bound is about $C_h < 20$ (Fig. 1, intersection between the dashed curve and the upper side of the hatched rectangle). According to Eq. (26) this implies that, if the transmission had been horizontal, each adult farmer would have converted on average up to 20 infantile HGs into. Interestingly, this vale is many times higher than the bound for oblique transmission (previous subsection), i.e., $C_o < 0.5$ (or 0.5 HGs converted per farmer on average). This shows again that oblique transmission is indeed much more powerful than horizontal transmission, because 40 times less conversions per farmer and generation are needed to attain the same front speed.

3.3. Vertical cultural transmission

Let us stress that our purpose is mainly to model oblique transmission (Section 3.1), but in doing so we have realized that the new framework makes it possible to improve previous models of horizontal and vertical transmission (by incorporating age structure), so it is worth to develop all three cases. For vertical transmission, some HGs mate with farmers and it is well-known from ethnographic observations that their children are always farmers (see, e.g., pp. 111 and 409 in Ref. [38] and p. 170 in Ref. [30]). Then, taking into account Eqs. (5), the evolution equations for the infantile (I) and adult (A) subpopulations of farmers (p) and HGs (q) are

$$\begin{cases} p_I(x,y,t+\tau) = F\, p_A(x,y,t)\left[1 + \eta\, \frac{q_A(x,y,t)}{p_A(x,y,t) + q_A(x,y,t)}\right] \\ p_A(x,y,t+\tau) = (1-m_I)\,\int_{-\infty}^{\infty}\int_{-\infty}^{\infty}\phi(\Delta_x,\Delta_y)p_I(x',y',t)d\Delta_x\,d\Delta_y \\ \qquad + (1-m_A)\,p_A(x,y,t) \\ q_I(x,y,t+\tau) = F_q\, q_A(x,y,t)\left[1 - \eta\, \frac{q_A(x,y,t)}{p_A(x,y,t) + q_A(x,y,t)}\right] \\ q_A(x,y,t+\tau) = (1-m_{Iq})\int_{-\infty}^{\infty}\int_{-\infty}^{\infty}\phi_q(\Delta_x,\Delta_y)\,q_I(x',y',t)d\Delta_x d\Delta_y \\ \qquad + (1-m_{Aq})\,q_A(x,y,t) \end{cases} \tag{32}$$

The first and third equations were derived using cultural transmission theory in Ref. [34], Eqs. (45), but there we consid-

ered the complete populations (i.e., $p(x,y,t)$ instead of $p_i(x,y,t)$ and $q(x,y,t)$ instead of $q_i(x,y,t)$ for $i = I, A$). Nevertheless, Eqs. (32) are more accurate because, as we have explained (footnote [3]), the age-structured model developed (Section 2) is more realistic for humans than the one without age structure used in Ref. [34]. Note that, in general, the absolute value of last term in the first of Eqs. (32) is not the same as that in the third equation. The reason is that we are dealing with vertical transmission (interbreeding), so reproduction must be taken into account and the fecundities (F and F_q) can be different in general (see Ref. [34] for a detailed derivation of the first and third of Eqs. (32)). As in the previous two subsections, we will find below that the front speed is independent of the of the parameters of population q (HGs) F_q, $\phi_q(\Delta_x, \Delta_y)$, m_{Iq} and m_{Aq}.

Repeating the same steps as in the previous subsections, we find that Eqs. (12)–(13) are replaced by

$$\eta\, \frac{p_A\, q_A}{p_A + \gamma q_A} = C_v\, p_A + O(2), \tag{33}$$

where

$$C_v = \eta \tag{34}$$

can be called the intensity of vertical cultural transmission, in the sense that if we neglect dispersal (i.e., $\phi(\Delta_x, \Delta_y) = 0$ except for $\Delta_x = 0$ and $\Delta_y = 0$) and fecundity ($F = 1$), so that we can focus our attention on the effect on cultural transmission, according to the first and third of Eqs. (32), when the first individuals of the invading population arrive to a region ($p_A \approx 0$),

$$\frac{p'_I - p_A}{p_A} = -\frac{q'_I - q_A}{p_A} \approx C_v, \tag{35}$$

so C_v gives the increase in the number density of invading individuals p (or the decrease in that of the autochthonous ones q) during one generation, per each pioneering adult of the invading population p. The oblique Eqs. (15)-(16), (19) and (21) are respectively replaced by

$$\begin{cases} p_I(x,y,t+\tau) = F(1+C_v)\, p_A(x,y,t) \\ p_A(x,y,t+\tau) = (1-m_I)\int_{-\infty}^{\infty}\int_{-\infty}^{\infty}\phi(\Delta_x,\Delta_y)\, p_I(x',y',t)d\Delta_x\,d\Delta_y \\ \qquad + (1-m_A)p_A(x,y,t), \end{cases} \tag{36}$$

$$\begin{cases} -e^{\lambda s\tau}\, w_I + F(1+C_v)w_A = 0 \\ (1-m_I)\,[p_e + (1-p_e)I_0(\lambda r)]w_I + \left[-e^{\lambda s\tau} + (1-m_A)\right]w_A = 0, \end{cases} \tag{37}$$

$$M = \begin{pmatrix} 0 & F(1+C_v) \\ (1-m_I)[p_e + (1-p_e)I_0(\lambda r)] & (1-m_A) \end{pmatrix}, \tag{38}$$

$$\begin{vmatrix} -\varrho & F(1+C_v) \\ (1-m_I)[p_e + (1-p_e)I_0(\lambda r)] & -\varrho + (1-m_A) \end{vmatrix} = 0. \tag{39}$$

and the front speed under horizontal cultural transmission is

$$s_v = \frac{\min}{\lambda > 0} \frac{\ln \frac{(1-m_A)+\sqrt{(1-m_A)^2+4(1-m_I)\, F\, (1+C_v)[p_e + (1-p_e)I_0(\lambda r)]}}{2}}{\lambda \tau}, \tag{40}$$

where s_v denotes the fronts speed under vertical cultural transmission. In Fig. 1 we plot this front speed as a blue, dashed-dotted line. Recall that for vertical transmission the allowed range of the cultural transmission intensity is $0 \le C_v \le 1$ (see the text below Eqs. (5)). The upper bound $C_v = 1$ implies, for the specific application of the spread of the Neolithic in Europe (Fig. 1), that vertical transmission can only have an effect of about 24% on the front speed, much less than for horizontal (45%) and oblique (190%) transmission (previous subsections).

Recall that the maximum observed speed of the Neolithic front in Europe is about $s_o = 1.3$ km (upper side of the hatched rectangle in Fig. 1). How does this maximum speed constrain the intensity of vertical cultural transmission? In Fig. 1, the intersection between the dashed-dotted curve and the upper side of the hatched rectangle implies that $C_v < 0.8$. According to Eq. (35), this implies that the increase in the number density of farmers due to interbreeding was up to 0.8 farmers per generation and adult farmer on average. This is much lower than that for horizontal transmission ($C_h < 20$). Thus we can conclude that vertical transmission can be much more powerful than horizontal transmission, but only in the sense that it requires much less conversions per generation to attain the same front speed (however, vertical transmission is not so powerful as oblique transmission, because $C_o < 0.5$). But vertical transmission is less powerful than horizontal tranmission as far as the maximum possible speed is concerned, as we explain in detail in the next paragraph.

We stress that vertical transmission is intrinsically limited by the upper bound $C_v = 1$ (see the text below Eqs. (5)) whereas C_o and C_h do not have any upper bound in principle (because there is not any limit *a priori* on the number of HGs to which a farmer can teach agriculture), and this implies that vertical transmission is unable to attain so fast rates as oblique and even horizontal transmission. For example, in Fig. 1 oblique transmission can lead to front speeds up to 3.13 km/yr (for $C_v \to \infty$), horizontal transmission up to 1.56 km/yr (for $C_h \to \infty$), and vertical transmission only up to 1.33 km/yr (for $C_v = 1$).

Our main conclusion is that the effect of oblique transmission on front propagation, which has been analyzed in this paper for the first time, is much more powerful than those of both horizontal and vertical transmission.

4. An additional case study

As an additional illustration we finally consider another Neolithic front, namely the spread of Khoi-khoi herders that took place since about 2,300 years until 1,100 years ago in southwestern Africa, at a speed between 1.4 and 3.3 km/yr according to archaeological data [48]. Ethnographic data on the mobility of pre-industrial herders imply that $p_e = 0.67$ and $r = 42$ km[8]. For the other parameters we use the same values as for pre-industrial farmers (as also done in Ref. [48]) because the reproductive dynamics of herders does not seem substantially different from that of herders according to the data available[9]. In Fig. 2 we plot the front speed predicted under oblique, horizontal and vertical transmission using the age-structured Eqs. (22), (31) and (40), respectively (in contrast, in Ref. [48] we considered only a horizontal model without age structure, which is less realistic as explained in footnote [3] above).

A relevant and unexpected result is that, in contrast to the Neolithic in Europe (Fig. 1), neither vertical nor horizontal transmission can explain the observed front speed of Khoi-khoi herders
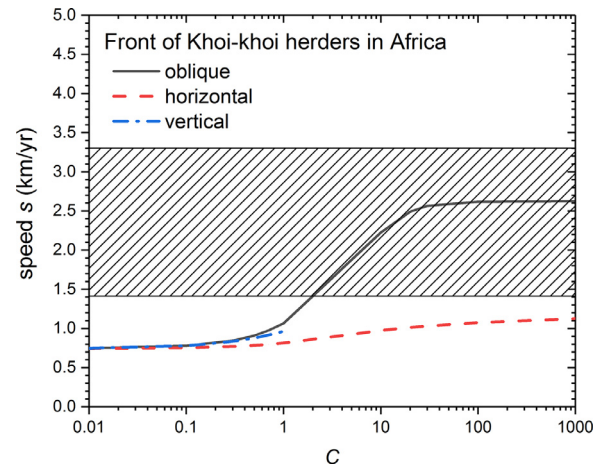
[8] In Ref. [26], note [32], the observed persistence $p_e = 0.38$ and mean-square displacement $\langle \Delta^2 \rangle = 1544$ km^2 of pre-industrial farmers (both of them obtained from ethnographic data) were used to estimate the value of r by applying that $\langle \Delta^2 \rangle = (1 - p_e) \, r^2$, which yields $r \approx 50$ km. We have applied these values in Sections. 2-3 for pre-industrial farmers. We use the same equation with the corresponding values from pre-industrial herders, i.e., $p_e = 0.67$ and $\langle \Delta^2 \rangle = 569$ km^2 [48], which yields $r \approx 42$ km.

[9] See the fecundities in Table 1 in Ref. [77] and the mortalities in Table 1 in Ref. [78]. These data distinguish between modes of subsistence but they do not refer to pioneering populations that expand their ranges (in contrast to the reproductive data used in Sections. 2-3). It would be therefore difficult to justify any extrapolations of the reproductive data in Refs. [77,78] to range expansions (because in the latter, the net population growth of the invading population is very fast at the leading edge of the front).

Fig. 2. Speed of the Neolithic front of Khoi-khoi herders in southwestern Africa as a function of the intensity C of cultural transmission (C_o for oblique, C_h for horizontal and C_v for vertical transmission). For all three curves, the parameter values are those representative of pre-industrial herders, namely $p_e = 0.67$, $r = 42$ km, $m_A = 0.49$, $m_I = 0.29$, $F = 2.69$ and $\tau = 16$ yr (see the main text). The hatched rectangle gives the observed front speed according to archaeological data (1.4-3.3 km/yr).

according to the new models, because both the vertical and horizontal cases predict too slow speeds (Fig. 2). Interestingly, there is only one cultural transmission mode that can explain such a fast front, namely oblique transmission (which, as seen above, is the most powerful one). This new result shows that the age-structured models introduced in this paper, besides making it possible to deal with oblique transmission, can lead to substantially improved predictions compared to previous models with horizontal [27,48] or vertical [34] transmission but without age structure (which, as seen in footnote [3], are less realistic).

The spread rate (front speed) of Khoi-khoi herders can be explained by assuming *oblique* transmission, but this implies not an upper bound (as in Fig. 1) but a lower bound for the intensity of oblique transmission C_o. The reason why there is not an upper bound is that in Fig. 2 the *oblique* model agrees with the observed range (hatched rectangle) for $C \to \infty$ (in contrast to Fig. 1). The reason why there is a lower bound is that in Fig. 2 the speed without cultural transmission ($C = 0$) is too slow to agree with the observed range (also in contrast to Fig. 1). The intersection of the lower side of the hatched rectangle with full line in Fig. 2 implies the lower bound $C_o > 2$ for oblique transmission. The implication in terms of human behavior is that in the Khoi-khoi expansion, each pioneering herder converted at least two HGs into herders by teaching herding to them (see Eq. (14)). Such a rate of cultural transmission may be reasonable in view of qualitative reports according to which herding is relatively simple to learn (compared with farming) [49–51].

A different possible explanation of the fastness of some Neolithic spread rates (alternative to cultural transmission) is biased dispersal, i.e., the assumption that farmers/herders are more likely to disperse into regions less populated by other farmers/herders [52]. Some years ago, it was proposed that genetics can make it possible to determine which explanation corresponds to reality, by identifying ancient parent-children pairs [53]. Later some such pairs buried in the same site were detected [54] and, very recently, a few pairs buried at different places have been also identified [55,56]. Unfortunately, their number is not yet sufficiently high to distinguish between both possible explanations.

According to Fig. 1, the Neolithic spread in Europe could have been mainly demic, i.e., with low levels of cultural transmission (because small values of C are consistent with the observed speed), and this agrees with the conclusions of ancient genetics [36,57].

In sharp contrast, according to Fig. 2 oblique cultural transmission had possibly an important effect on the Khoi-khoi expansion (because low values of C are inconsistent with the observed speed). Such a possible importance of cultural transmission in the spread of the Khoi-khoi front agrees with the views of some experts on African archaeology [58–60] and researchers on human range expansions [39].

5. Conclusions

We have developed a model of interacting populations with age structure and applied it to derive the speed of fronts under *oblique* cultural transmission. Previous models of front propagation considered only vertical and horizontal (but not oblique) transmission, and they ignored age structure. We have also built models with horizontal and vertical transmission and age structure. In this way, we have presented what we believe are the first comparisons of front speeds under oblique, horizontal and vertical cultural transmission (Figs. 1-2).

Our main result is that the most powerful mechanism is oblique transmission. For a given value of the cultural transmission intensity, it yields the fastest fronts because in oblique transmission culture is transmitted to children before their dispersal, and these new members of the invading population increase its front speed. Another new result is that for a given value of the cultural transmission intensity, vertical transmission yields faster fronts than horizontal transmission (Figs. 1-2). However, the intensity of vertical transmission is limited ($C_v \leq 1$, see Section 1) and this makes it possible for horizontal transmission (if sufficiently intense, $C_h \to \infty$) to yield speeds faster than the maximum possible one (i.e., for $C_v = 1$) under vertical transmission (Figs. 1-2).

According to the data available, cultural transmission is not necessary to explain the observed speed of the Neolithic front in Europe (Fig. 1 for $C = 0$). In contrast, cultural transmission can explain the speed of the Khoi-khoi expansion, which is clearly faster according to the archaeological dates available. However, neither vertical nor horizontal transmission are enough to explain such a fast rate. Oblique transmission is apparently necessary, unless other effects (such as biased dispersal [52]) are assumed.

Will it be possible to determine if cultural transmission in Neolithic front propagation existed and, if so, whether it was oblique, horizontal and vertical? The existence of cultural transmission has been already shown by geneticists for the spread of the Neolithic in Europe, because some genetic markers persisted (although many did not) [36]. In principle, it could be possible to determine if the transmission was vertical or not by comparing the genetic markers of individuals buried in the same site. For example, if both the mitochondrial and Y-chromosome haplogroups of an individual were different from the rest, this would be strong evidence that cultural transmission was not vertical, i.e., not due to interbreeding (because the mitochondrial and Y-chromosome haplogroups are inherited from the mother and father, respectively). It will be more difficult to distinguish between oblique and horizontal transmission, but this could also be possible if the ages of individuals as well as their haplogroups were determined (this seems possible in principle because, as we have mentioned above, the ages of prehistoric individuals have been determined in some studies [61]). In principle this could make it possible to determine if HGs (with their characteristic genetic markers) joined the sites of farmers as infantile individuals (oblique transmission) or adults (horizontal transmission).

In this paper we have used a simple dispersal kernel, Eq. (10), in which individuals either stay near their birthplace ($\Delta = 0$) or move a given distance ($\Delta = r$). The reason is that this makes equations easier to handle, and this facilitates to focus our attention on the main point of this paper (cultural transmission with age structure, as necessary to deal with oblique transmission). In future research it will be of interest to analyze how the main conclusions would change if we did not use such a simple kernel. Previous work has shown that continuous kernels (Gaussian, Laplacian, etc.) are not appropriate for human expansions because (similarly to differential equations based on ordinary diffusion) they yield substantial errors if compared to the most precise approach possible, namely dispersal distances and probabilities recorded directly from ethnographic observations [24]. Thus future research should use, instead of the kernel (10), the complete set of dispersal distances and probabilities (i.e., histograms directly recorded by ethnographic fieldwork)[10].

Besides the examples of Neolithic spread considered in this paper, there are other case studies to which our new models can be applied, including the spread of the Neolithic in Scandinavia (a rather slow front) [62], the Western Mediterranean (a very fast front) [63], domesticated rice in eastern Asia [64], maize agriculture in America [65], Bantu expansions of African farmers [51], etc. Another very interesting avenue of future applications is the explanation of genetic clines (i.e., gradients) caused by cultural transmission effects on the propagation of population fronts [19]. The only existing model of genetic clines based cultural transmission theory has no age structure and assumes interbreeding, i.e., vertical cultural transmission [57]. Clearly it would be of interest to predict the shape of genetic clines using our age-dependent models of oblique, horizontal and vertical transmission. Therefore, the models in this paper have both archaeological and genetic applications in all of the Neolithic spread case studies listed above. They are also of interest in the study of many non-Neolithic fronts. Two examples are the spread of modern humans [66,67,68] in Europe (where they interbred with Neanderthals) and Asia (where they interbred both with Neanderthals and Denisovans) [69,70]. More recent major human expansions include that of the Yamnaya herders from the Caspian steppes about 4,500 yr ago, which caused a major genetic turnover and is considered to have spread Indo-European languages [71]. The quantifications of the roles of cultural transmission in its different forms (vertical, horizontal and oblique) in the front spread rates and genetic clines of these and other human expansions are interesting open problems. Non-human applications are also possible because cultural transmission has been widely studied in other animals such as birds [72], rodents [73], primates [74], etc.

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.

Acknowledgements

References

[1] Ebert U, van Saarloos W. Front propagation into unstable states: Universal algebraic convergence towards uniformly translating pulled fronts. Physica D 2000;146:1–99.

---

[10] Note that even without cultural transmission ($C = 0$) we cannot use previous results (including those based on the complete kernel) because they did not use an age-structured model (as necessary for oblique transmission, and more realistic for horizontal and vertical transmission). In other words, previous models [27,34,48,51,79] used only a net reproduction rate R_0 rather than the fecundity F and mortalities m_I and m_A applied in the present paper. For this reason, even for $C = 0$ the previous models without age structure will yield different results than the new models with age structure.

[2] van Saarloos W. Front propagation into unstable states. Phys Rep 2003;386:29–222.

[3] Fort J, Méndez V. Wavefronts in time-delayed systems. Theory and comparison to experiment. Rep Progr Phys 2002;65:895–954.

[4] Fort J, Pujol T. Progress in front propagation research. Rep Prog Phys 2008;71(086001).

[5] Khain E, Sander LM. Dynamics and pattern formation in invasive tumor growth. Phys Rev Lett 2006;96(188103).

[6] Fort J, Solé RV. Accelerated tumor invasion under non-isotropic cell dispersal in glioblastomas. New J Phys 2013;15(055001).

[7] Yin J, McCaskill JS. Replication of viruses in a growing plaque: a reaction-diffusion model. Biophys J 1992;61:1540–9.

[8] Fort J, Méndez V. Time-delayed spread of viruses in growing plaques. Phys Rev Lett 2002;89(178101).

[9] Fisher RA. The wave of advance of advantageous genes. Ann Eugen (London) 1937;7:355–69.

[10] Vlad JO, Moran M, Tsuchiya M, Cavalli-Sforza LL, Oefner PJ, Ross J. Neutrality condition and response law for nonlinear reaction-diffusion equations, with application to population genetics. Phys Rev E 2002;65(061110).

[11] Bernabeu-Aubán J, Barton CM, Pardo-Gordó S, Bergin SM. Modelling initial Neolithic dispersal. The first agricultural groups in the Western Mediterranean. Ecol. Modelling 2015;307:22–31.

[12] Barcelo JA, del Castillo F, editors. Simulating prehistoric and ancient worlds. Cham: Springer; 2016.

[13] Ammerman AJ, Cavalli-Sforza LL. A population model for the diffusion of early farming in Europe. In: Renfrew C, editor. The explanation of culture change: models in prehistory. London: Duckworth; 1973. p. 343–57.

[14] Baggaley AW, Sarson GR, Shukurov A, Boys RJ, Golightly A. Bayesian inference for a wave-front model of the neolithization of Europe. Phys Rev E 2012;86(016105).

[15] Fort J, Pujol T. Time-delayed fronts from biased random walks. New J Phys 2007;9(234).

[16] Fort J, Pérez-Losada J, Suñol JJ, Escoda L, Massaneda JM. Integro-difference equations for interacting species and the Neolithic transition. New J Phys 2008;10(043045).

[17] Isern N, Fort J. Anisotropic dispersion, space competition and the slowdown of the Neolithic transition. New J Phys 2010;12(123002).

[18] Patterson MA, Sarson GR, Sarson HC, Shukurov A. Modelling the Neolithic transition in a heterogeneous environment. J Arch Sci 2010;37:2929–37.

[19] Ammerman AJ, Cavalli-Sforza LL. The neolithic transition and the genetics of populations in Europe. New Jersey: Princeton University Press; 1984.

[20] Fort J, Méndez V. Time-delayed theory of the Neolithic transition in Europe. Phys Rev Lett 1999;82:867–70.

[21] Kolmogorov AN, Petrovsky IG, Piskunov NS. A study of the diffusion equation with increase in the amoount of substance, and its application to a biological problem. Bull Univ Moscow, Ser Int A 1937;1:1–26.

[22] Lotka AJ. Elements of mathematical biology. New York: Dover; 1956.

[23] Cavalli-Sforza LL. The distribution of migration distances: models and applications to genetics. In: *Human displacements*, monaco, editions sciences humaines; 1962. p. 139–58.

[24] Isern N, Fort J, Pérez-Losada J. Realistic dispersion kernels applied to cohabitation reaction-dispersion equations. J Stat Mechs 2008;2008:P10012.

[25] Murray JD. Mathematical biology. Berlin: Springer-Verlag; 1993.

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

[27] Fort J. Synthesis between demic and cultural diffusion in the Neolithic transition in Europe. Proc Natl Acad Sci USA 2012;109:18669–73.

[28] Fort J, Jana D, Humet J. Multidelayed random walks: theory and application to the neolithic transition in Europe. Phys Rev E 2004;70(031913).

[29] Renfrew C. From molecular genetics to archaeogenetics. PNAS 2001;98:4830–2.

[30] Bentley RA, Layton RH, Tehrani J. Kinship, marriage, and the genetics of past human dispersals. Hum Biol 2009;81:159–79.

[31] Rendine S, Piazza A, Cavalli-Sforza LL. Simulation and separation by principal components of multiple demic expansions in Europe. American Naturalist 1986;128:681–706.

[32] Barbujani G, Sokal RD, Oden NL. Indo-European origins: a computer simulation test of five hypothesis. Am J Phys Anthropol 1995;96:109–32.

[33] Currat M, Excoffier L. The effect of the Neolithic expansion on European molecular diversity. Proc Roy Soc B 2005;272:679–88.

[34] Fort J. Vertical cultural transmission effects on demic front propagation: Theory and application to the Neolithic transition in Europe. Phys Rev E 2011;83(056124).

[35] Cavalli-Sforza LL, Feldman MW, Chen KH, Dornbusch SM. Theory and observation in cultural transmission. Science 1982;218:19–27.

[36] Bramanti B, et al. Genetic discontinuity between local hunter-gatherers and central Europe^{\prime}s first farmers. Science 2009;326:137–40.

[37] Cavalli-Sforza LL, Feldman MW. Cultural transmission and evolution: A quantitative approach. New Jersey: Princeton University Press; 1981.

[38] Cavalli-Sforza LL. African Pygmies. Orlando: Academic Press; 1986.

[39] Diamond J, Bellwood P. Farmers and their languages: the first expansions. Science 2003;300:597–602.

[40] Hewlett BS, Cavalli-Sforza LL. Cultural transmission among Aka pygmies. Amer. Anthropol 1986;88:922–34.

[41] Neubert M, Caswell H. Demography and dispersal: calculation and sensitivity analysis of invasion speed for structured populations. Ecology 2000;81:1613–28.

[42] Caswell H. Matrix population models. Sunderland: Sinhauer; 1989.

[43] Amor D, Fort J. Fronts from two-dimensional dispersal kernels: beyond the non-overlapping generations model. Phys Rev E 2009;80(051918).

[44] Pérez-Losada J, Fort J. Age-dependent mortality, fecundity and mobility effects on front speeds: theory and application to the Neolithic transition. J Stat Mechs 2010;2010:P11006.

[45] Stauder J. The Majangir: ecology and society of a southwest Ethiopian people. Cambridge: Cambridge University Press; 1971.

[46] Fort J, Méndez V. Reaction-diffusion waves of advance in the transition to agricultural economics. Phys Rev E 1999;60:5894–901.

[47] Pinhasi R, Fort J, Ammerman AJ. Tracing the origin and spread of agriculture in Europe. PLoS Biology 2005;3(e410):2220–8.

[48] Jerardino A, Fort J, Isern N, Rondelli B. Cultural diffusion was the main driving mechanism of the Neolithic transition in Southern Africa. PLos One 2014;9(e113672).

[49] Lee RB. The !Kung San. Men, women and work in a foraging society. Cambridge: Cambridge University Press; 1979. p. 409–12.

[50] Sorensen L. New theoretical discourses in the discussion of the Neolithisation process in South Scandinavia during the late 5th and early 4th millennium BC - an identification of learning processes, communities of practise and migrations. Documenta Praehistorica 2016;43:209–34.

[51] Isern N, Fort J. Assessing the importance of cultural diffusion in the Bantu spread into southeastern Africa. PLoS One 2019;14(e0215573).

[52] Fort J. Biased dispersal can explain fast human range expansions. Sci Rep 2020;10(9036).

[53] Fort J. Demic and cultural diffusion propagated the Neolithic transition across different regions of Europe. J Roy Soc Interface 2015;12(20150166).

[54] Monroy JM, Jakobsson M, Günther T. Estimating genetic kin relationships in prehistoric populations. PLoS One 2018;13(e0195491).

[55] Sánchez-Quinto F;, Malmström H;, Fraser M, Girdland-Flink L, Svensson E M, Simoes LG, et al. Megalithic tombs in western and northern Neolithic Europe were linked to a kindred society. Proc Natl Acad Sci U.S. 2019;116:9469–74.

[56] Mittnik A, Massy K, Knipper C, Wittenborn, Friedrich RF, et al. Kinship-based social inequality in Bronze age Europe. Science 2019;366:731–4.

[57] Isern N, Fort J, Rioja V. The ancient cline of haplogroup K implies that the Neolithic transition in Europe was mainly demic. Sci Rep 2017;7(11229).

[58] Sadr K. A short history of early herding in southern Africa. In: Pastoralism in Africa: past, present and future. New York and Oxford: Berghahn Books; 2013. p. 171–97.

[59] Smith AB. African herders: emergence of pastoral traditions. Walnut Creek: Alta Mira Press; 2005.

[60] Kinahan J. Alternative views on the acquisition of llivestock by hunter-gatherers in southern Africa. S Afr Archaeol Bull 1996;51:106–8.

[61] Eshed V, Gopher A, Gage TB, Hershkovitz I. Has the transition to agriculture reshaped the demographic structure of prehistoric populations? New evidence from the Levant. Am J Phys Anthropol 2004;124:315–29.

[62] Fort J, Pareta MM, Sorensen L. Estimating the relative importance of demic and cultural diffusion in the spread of the Neolithic in Scandinavia. J R Soc Interface 2018;15(20180597).

[63] Isern N, Zilhao J, Fort J, Ammerman AJ. Modeling the role of voyaging in the coastal spread of the early Neolithic in the West Mediterranean. PNAS 2017;114:897–902.

[64] Cobo JM, Fort J, Isern N. The spread of domesticated rice in eastern and southeastern Asia was mainly demic. J Arch Sci 2019;101:123–30.

[65] Blake M. Maize for the gods. Understanding the 9,000-year history of corn. Oakland: University of California Press; 2015.

[66] Wakano JY, Gilpin W, Kadowaki S, Feldman MW, Aoki K. Ecocultural range–expansion scenarios for the replacement or assimilation of Neanderthals by modern humans. Theor Popul Biol 2019;119:3–14.

[67] Romanowska I, Gamble C, Bullock S, Sturt F. Dispersal and the Movius line: testing the effect of dispersal on population density through simulation. Q Int 2017;431:53–63.

[68] Wakano JY, Kadowaki S. Application of the ecocultural range expansion model to modern human dispersals in Asia. Q Int 2021. doi:10.1016/j.quaint.2020.12.019.

[69] Fu Q, Li H, Moorjani P, Jay F, Slepchenko SM, Bondarev AA, Johnson PLF, et al. Genome sequence of a 45,000-year old modern human from western Siberia. Nature 2014;514:445–9.

[70] Browning SR, Browning BL, Zhou Y, Tucci S, Akey JM. Analysis of human sequence data reveals two pulses of archaic Denisovan admixture. Cell 2018;173:1–9.

[71] Haak W, Lazaridis I, Patterson N, Rohland N, Mallick S, Llamas B, Brandt G, et al. Massive migration from the steppe was a source for Indo-European languages in Europe. Nature 2014;522:207–11.

[72] Aplin LM, Farine DR, Morand-Ferron J, Cokburn A, Thornton A, Sheldon BC. Experimentally induded innovations lead to persistent culture via conformity in wild birds. Nature 2015;518:538–41.

[73] Barker AJ, Veviurko G, Bennett NC, Hart W, Mograby DWL, Lewin GR. Cultural transmission of vocal dialect in the naked mole-rat. Science 2021;371:503–7.

[74] Biro D, Inoue-Nakamura N, Tonooka RYamakoshi, Sousa GC, Matsuzawa T. Cultural innovation and transmission of tool use in wild chimpanzees. Anim Cogn 2003;6:213–23.

[75] Charbonneau H, Desjardins B, Légaré J, Denis H. The population of the St. Lawrence Valley, 1608-1760. In: A population history of North America. Cambridge: Cambridge University Press; 2000. p. 99–142.

[76] Engelhardt SC, Bergeron P, Gagnon A, Dillon L, Pelletier F. Using geographic distance as a potential proxy for help in the assessment of the grandmother hypthesis. Curr Biol 2019;29:651–6.

[77] Sellen DW, Mace R. Fertility and mode of subsistence: a phylogenetic analysis. Curr Anthropol 1997;38:787–889.

[78] Sellen DW, Mace R. A phylogenetic analysis of the relationship between sub--adult mortality and mode of subsistence. J Biosoc Sci 1999;31:1–16.

[79] Fort J, Pareta MM. Long-distance dispersal effects and Neolithic waves of advance. J Arch Sci 2020;119(105148).