Cultural transmission in human range expansions and Neolithic estimations

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Cultural transmission

Are Lotka-Volterra equations adequate?

Population numbers after *(P')* and before *(P)* cultural transmission (during 1 generation)

$$\begin{cases} \text{number of farmers } (F): \quad P'_F = P_F + \alpha P_F P_H & (1) \\ \text{number of hunter} - \text{gatherers } (H): P'_H = P_H - \alpha\, P_F P_H & (2) \end{cases}$$

Problem:

Number of HGs converted per farmer according

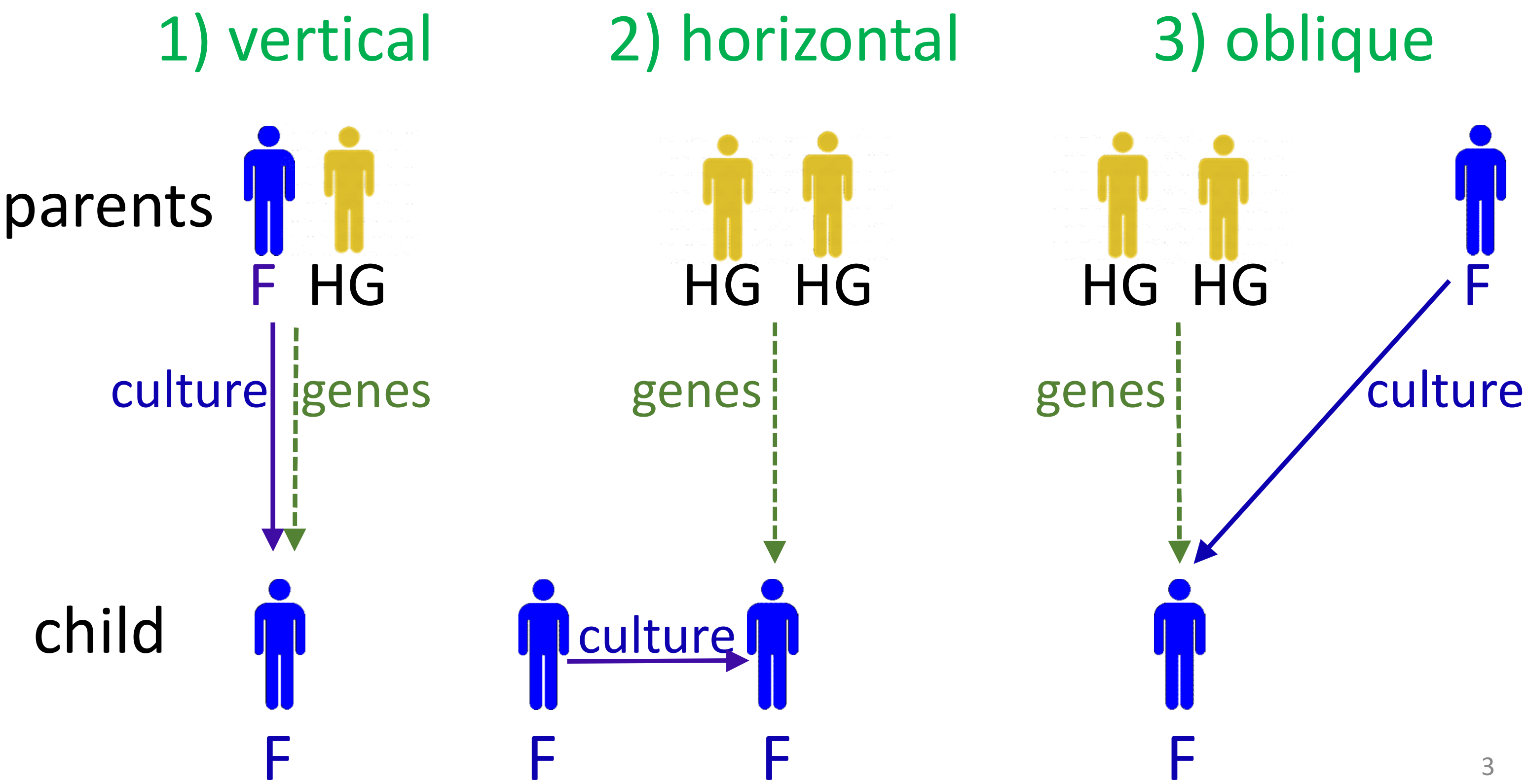
to Eq. (2) $= \frac{P_H - P'_H}{P_F} = \alpha P_H \to \infty!$ No maximum!

if $P_H \to \infty$

Fort, PNAS (2012)

Cultural transmission

3 types



Horizontal cultural transmission

In order to analyze archaeological data, vertical transmission is not enough.

Cavalli-Sforza & Feldman, *Cultural transmission and evolution* (1981)

$n =$ number of teachers that a HG contacts during his/her lifetime.

[If n were proportional to $P_F + P_H$, we would obtain Lotka-Volterra eqs., but according to ethnographic data n is roughly the same for many populations (Dunbar, 1993)]

$$\frac{P_F}{P_F+P_H} = u = \text{proportion of F-teachers of a HG.}$$

$$n\frac{P_F}{P_F+P_H} = n\,u = \text{number of F-teachers of a HG.}$$

$q =$ probability that a HG becomes F due to contact with a single F teacher.

$$1-\underbrace{(1-q)^{nu}}_{\text{probab. not F}} = \text{probability that a HG becomes F during his lifetime}$$

$1-(1-q)^{nu} \approx nqu = fu$ if $q \ll 1$, with $f \equiv nq$

Number of HGs who become Fs per generation $= fuP_H$

Horizontal cultural transmission

number of HGs who become Fs $= fuP_H = f\frac{P_F P_H}{P_F+P_H}$

per generation

$u = \frac{P_F}{P_F + P_H}$

$$\begin{cases} P_F' = P_F + f\frac{P_F P_H}{P_F + P_H} \\ P_H' = P_H - f\frac{P_F P_H}{P_F + P_H} \end{cases}$$

Number of HGs converted per farmer:

$$\frac{P_H - P_H'}{P_F} = f\frac{P_H}{P_F + P_H} \to f$$

if $P_H \to \infty$

There is a maximum.

In contrast, for Lotka-Volterra eqs.:

$$\begin{cases} P_F' = P_F + \alpha P_F P_H \\ P_H' = P_H - \alpha P_F P_H \end{cases}$$

$$\frac{P_H - P_H'}{P_F} = \alpha P_H \to \infty!$$

No maximum.

if $P_H \to \infty$

Horizontal cultural transmission

Limitation of these equations (noted by L. L. Cavalli-Sforza, 2011)

$$\begin{cases} P_F' = P_F + f\,\dfrac{P_F P_H}{P_F + P_H} \\ P_H' = P_H - f\,\dfrac{P_F P_H}{P_F + P_H} \approx P_H - f\,P_H = (1-f)\,P_H > 0 \rightarrow f \le 1 \end{cases}$$

if $P_F \gg P_H$

$$\begin{cases} P_F' = P_F + f\,\dfrac{P_F P_H}{P_F + P_H} \\ P_H' = P_H - f\,\dfrac{P_F P_H}{P_F + P_H} \approx P_H - f\,P_F \rightarrow \dfrac{P_H - P_H'}{P_F} = f \end{cases}$$

if $P_H \gg P_F$

each farmer can at most convert a single HG in their lifetime!

Horizontal cultural transmission

A generalization avoids this limitation:

·We have assumed that a HG is equally likely to learn from Fs or HGs, so that:

$$\text{number of F-teachers per HG} = n\frac{P_F}{P_F+P_H}$$

·We now assume that a HG contacts only (for learning purposes) a portion α of his F neighbors and a portion β of his HG neighbors, then:

$$\text{number of F-teachers per HG} = n\frac{\alpha\, P_F}{\alpha\, P_F+\beta P_H} = n\frac{P_F}{P_F+\gamma P_H}$$

$\gamma = \beta/\alpha$

Thus:

if $P_F \gg P_H$

$$P_H' = P_H - f\frac{P_F P_H}{P_F+\gamma P_H} \approx P_H - f\ P_H = (1-f)\ P_H > 0 \rightarrow f \leq 1$$ as before, but:

$$P_H' = P_H - f\frac{P_F P_H}{P_F+\gamma P_H} \approx P_H + \frac{f}{\gamma}\ P_F \rightarrow \frac{P_H - P_H'}{P_F} = \frac{f}{\gamma}\ \text{not} \leq 1$$, so **a F may convert >1 HG**.

if $P_H \gg P_F$

Horizontal cultural transmission

$$\begin{cases} P'_F = P_F + f\,\dfrac{P_F P_H}{P_F + \gamma P_H} \approx P_F + C\,P_F \\ P'_H = P_H - f\,\dfrac{P_F P_H}{P_F + \gamma P_H} \approx P_H - C\,P_F \end{cases}$$

$C = \frac{f}{\gamma}$

the front speed depends only on C, not on f and γ separately

when the first farmers arrive $(P_F \approx 0)$

For frequency-dependent transmission, f is usually replaced by $f + h\left(2\frac{P_F P_H}{P_F+P_H} - 1\right)$ [1,2]

but $\frac{P_F P_H}{P_F+P_H} \approx P_F$ for $P_F \approx 0$, so it leads to a 2nd-order term in the eqs. above.

Thus the only change is that $C = \frac{f}{\gamma}$ is replaced by $C = \frac{f-h}{\gamma}$.

So the Neolithic results (next slides) do not change.

[1] Boyd & Richerson 1985

[2]Henrich 2001: h=conformist, f=direct and indirect (e.g., prestige) biases.

Application to the Neolithic (F=number of farmers/km^2)

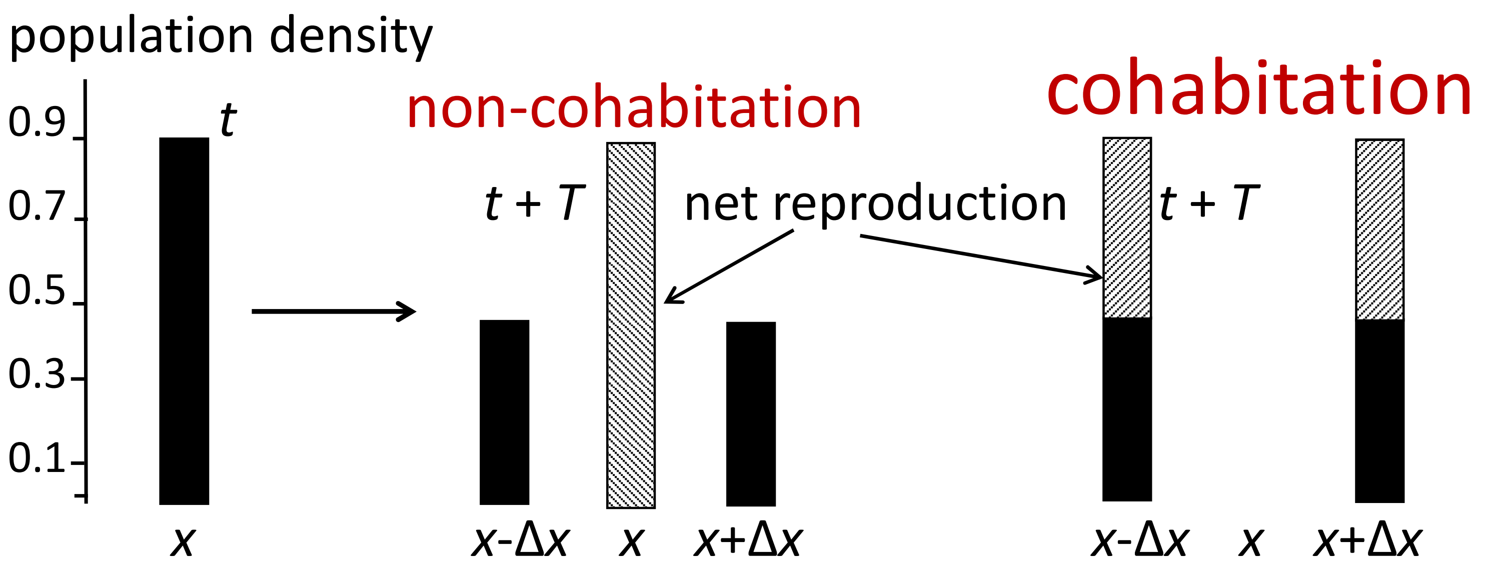
(1) Non-cohabitation eq.: $F(x,y,t+T)-F(x,y,t)=$

$$\int_{-\infty}^{\infty}\int_{-\infty}^{\infty} F(x+\Delta_x, y+\Delta_y, t)\ \phi_F(\Delta_x,\Delta_y)\ d\Delta_x\ d\Delta_y - F(x,y,t) + R_T[F(x,y,t)] - F(x,y,t)$$

This leads to Fisher's eq. but makes substantial errors (up to 50%, Isern et al. 2008)

(2) Cohabitation equation:

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



Population densities: *F* = farmers, *H* =HGs

$$\begin{cases} F(x,y,t+T) = \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} \tilde{F}(x+\Delta_x, y+\Delta_y, t)\,\phi_F\left(\Delta_x,\Delta_y\right)\,d\Delta_x\,d\Delta_y \\ H(x,y,t+T) = \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} \tilde{H}(x+\Delta_x, y+\Delta_y, t)\,\phi_H\left(\Delta_x,\Delta_y\right)\,d\Delta_x\,d\Delta_y \end{cases}$$

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

$$\tilde{H}(x,y,t) \equiv R_T[H(x,y,t)] - f\,\frac{R_T[F(x,y,t)]R_T[H(x,y,t)]}{R_T[F(x,y,t)] + \gamma\,R_T[H(x,y,t)]}$$

$$R_T[F(x,y,t)] = \frac{e^{a_F T}\,K_F\,F(x,y,t)}{K_F+\left(e^{a_F T}-1\right)F(x,y,t)}$$

$$R_T[H(x,y,t)] = \frac{e^{a_H T}\,K_H\,H(x,y,t)}{K_H+\left(e^{a_H T}-1\right)H(x,y,t)}$$

Fort, *PNAS* 2012

Application to the Neolithic

The front speed for the previous set of equations is

$$\min_{\lambda > 0} \frac{a_F\, T + \ln\left[(1+C)\left(\sum_{j=1}^{M} p_j\, I_0(\lambda r_j)\right)\right]}{T\lambda}, \qquad C = \frac{f}{\gamma}$$

where

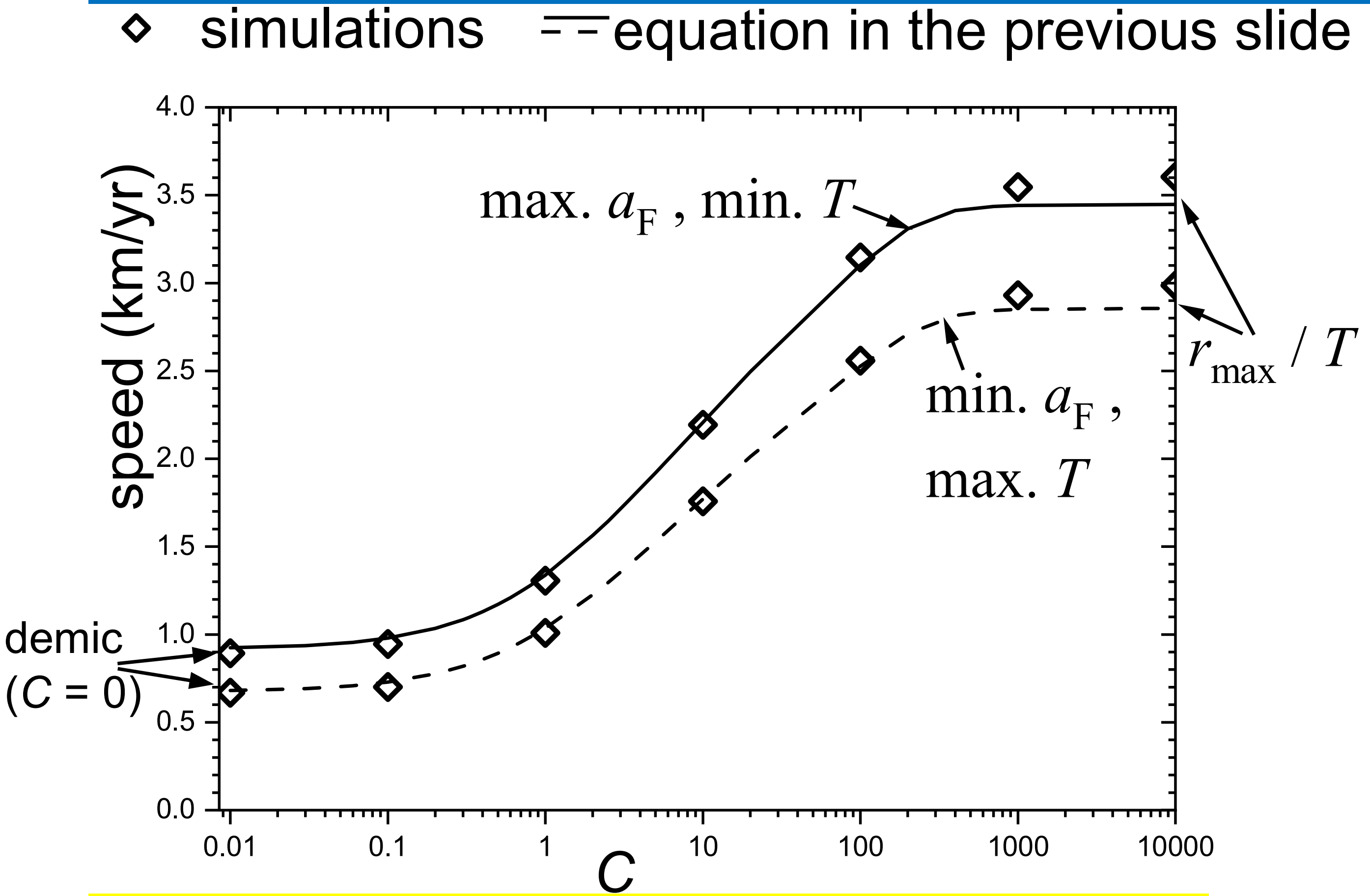
$I_0(\lambda r) = \frac{1}{2\pi}\int_0^{\infty} d\theta\, \exp[\lambda\, r\, cos\theta]$ =modified Bessel function of the first kind and order zero,

$\{p_j, r_j\}$ is the demic dispersal kernel of farmers $\phi_F\,(\Delta_x, \Delta_y)$.

This result is valid for any range expansion, not only for the Neolithic.

Fort, *PNAS* 2012

Application to the Neolithic



Parameter values used (from ethnographic data):

$a_F = 0.023 - 0.033\ yr^{-1}$

$T = 29 - 35\ yr$

$\{p_j\}$={0.42; 0.23; 0.16; 0.08; 0.07; 0.02; 0.01; 0.01}

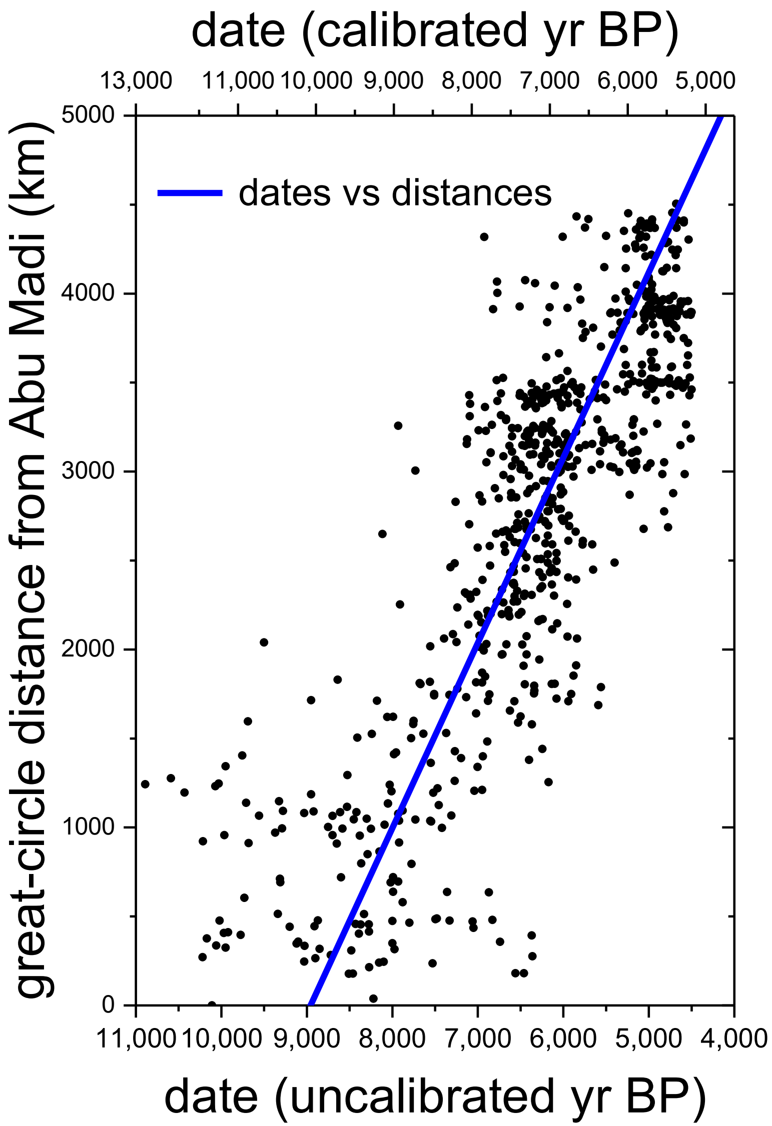
$\{r_j\}$={2.3, 7.3, 15, 25, 35, 45, 55, 100} km

$C = \frac{f}{\gamma}$ = intensity of cultural transmission

Fort, *PNAS* (2012)

How can we compare this theory to data? Next slides

Application to the Neolithic in Europe



What is the observed speed?

0.9-1.3 km/yr

735 sites in Europe & Near East

r = 0.83

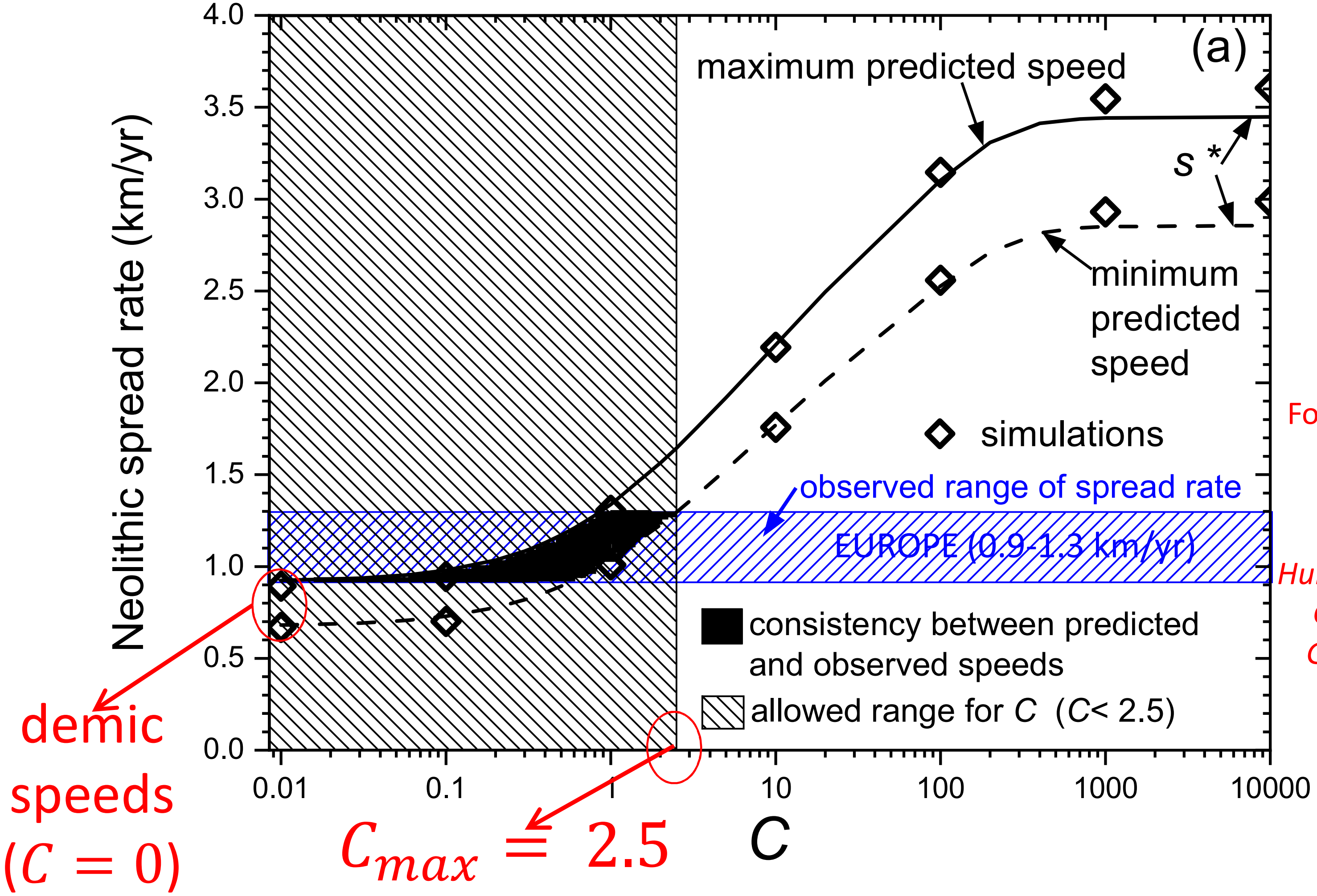
(highest-*r* origin)

dates vs distances

great circles & shortest paths

Pinhasi, Fort & Ammerman, *PLoS Biol.* (2005)

Application to the Neolithic in Europe

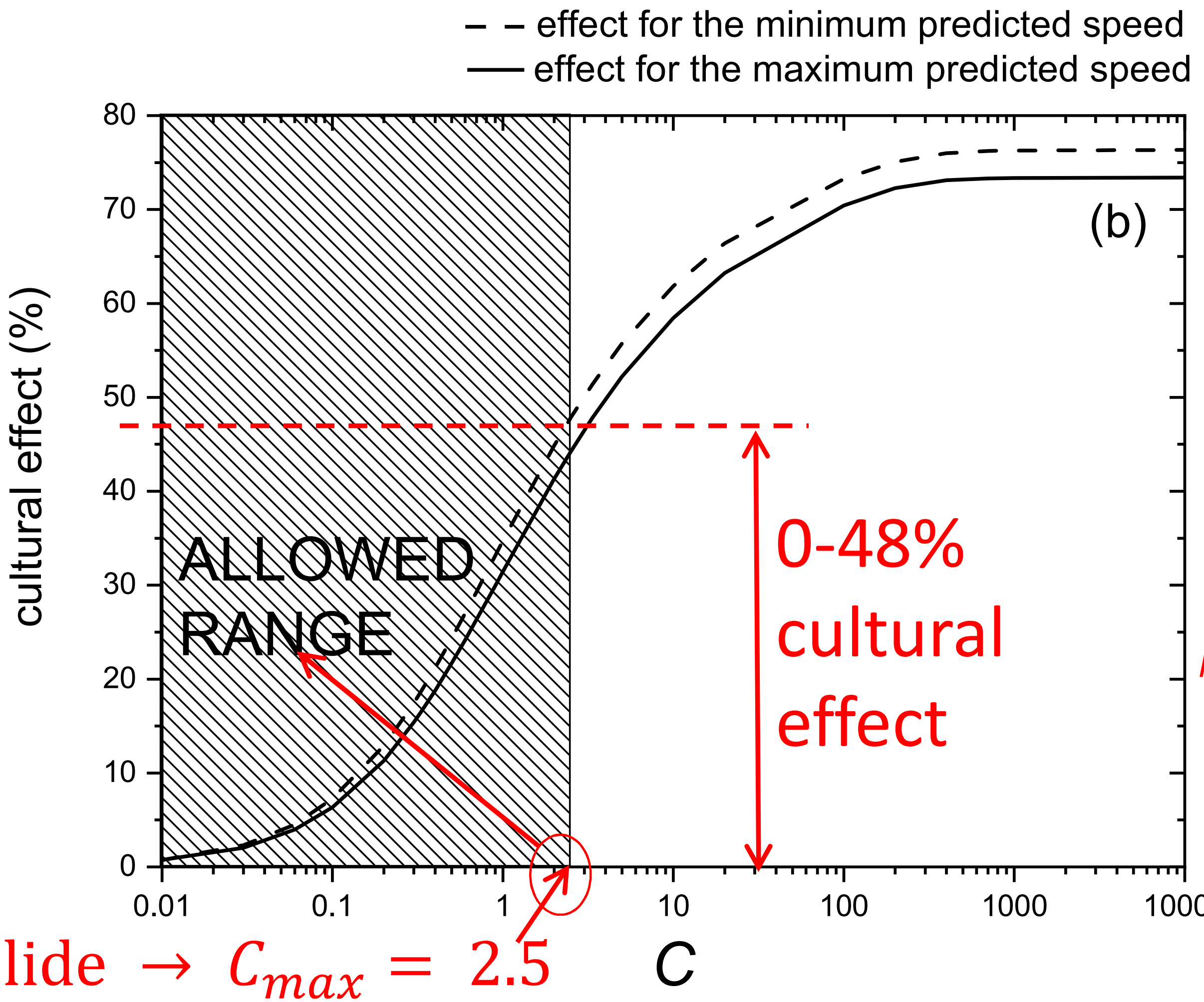


Fort, *PNAS* (2012)

Fort, *Hum. Popul. Gen. & Genom.* 2022

Application to the Neolithic in Europe

Effect of cultural diffusion (%) = (speed – demic speed) /speed · 100



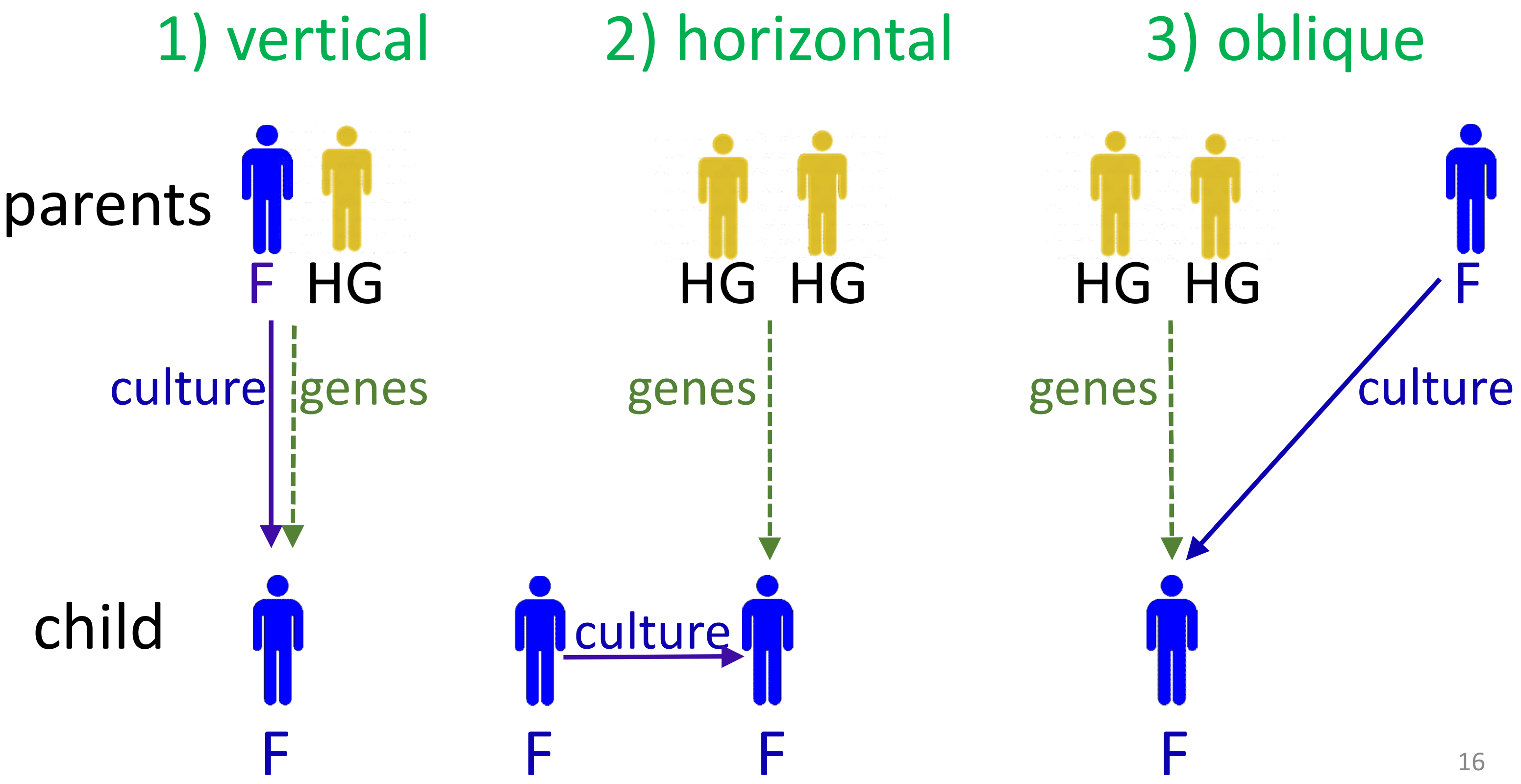
Fort, *PNAS* (2012)

Fort, *Hum. Popul. Gen. & Genom.* 2022

previuos slide → $C_{max} = 2.5$

Cultural transmission

3 types



Vertical cultural transmission

We will use it to analyze genetic data

Equations are very similar to the horizontal case. Only 1 parameter (not 2):

HORIZONTAL $C = \frac{f}{\gamma}$

$$\begin{cases} P'_F = P_F + f\dfrac{P_F P_H}{P_F + \gamma P_H} \approx P_F + C\, P_F \\ P'_H = P_H - f\dfrac{P_F P_H}{P_F + \gamma P_H} \approx P_H - C\, P_F \end{cases}$$

VERTICAL* $C = \eta$

$$\begin{cases} P'_F = P_F + \eta\dfrac{P_F P_H}{P_F + P_H} \approx P_F + C\, P_F \\ P'_H = P_H - \eta\dfrac{P_F P_H}{P_F + P_H} \approx P_H - C\, P_F \end{cases}$$

when the first farmers arrive ($P_F \approx 0$). So **the speed is the same**.

If $P_H \approx 0 \rightarrow P'_H = P_H - C\, P_H \rightarrow C$<1 for vertical trans.

In the previous slides, $C_{max} = 2.5$. This is why we have used horizontal trans.

*3 derivations: (1) Cavalli-Sforza & Feldman 1981, p.97; (2) Fort, Phys. Rev. 2011; (3) same derivation as for the horizontal case (previous slides) with *n*= potential mates instead of teachers

Vertical cultural transmission

SIMULATIONS: Grid of square cells. Initially farmers only at the cell containing the oldest site in Upper Mesopotamia (Abu Hureyra) with a %K such that we obtain the observed %K (47.4%) at the average location and date of the 15 early farmers in Upper Mesopotamia whose mtDNA is known.

All other grid cells are initially empty of farmers and with HGs at their saturation density.

At each node in the grid and time step (1 generation=32 yr), we compute 3 processes:

(1) Dispersal: 38% do not migrate, the rest 50 km (both from ethnography). Migration threshold: migration only if the farmer density is > 0.06 farmers/km^2, from archaeology and ethnography.

(2) Cultural transmission: next slide.

(3) Reproduction: next slide.

Vertical cultural transmission

(2) Cultural transmission:

P_N =farmers who *have* haplogroup K.

P_X = farmers who *do not have* haplogroup K.

P_{HG} = hunter-gatherers (all without haplogroup K).

$$\%K = \frac{P_N}{P_N + P_X}$$

Vertical transmission =Interbreeding: $couples\ HN = C\frac{P_{HG}P_N}{P_{HG}+P_N+P_X}$

$$couples\ HX = C\frac{P_{HG}P_X}{P_{HG}+P_N+P_X}$$

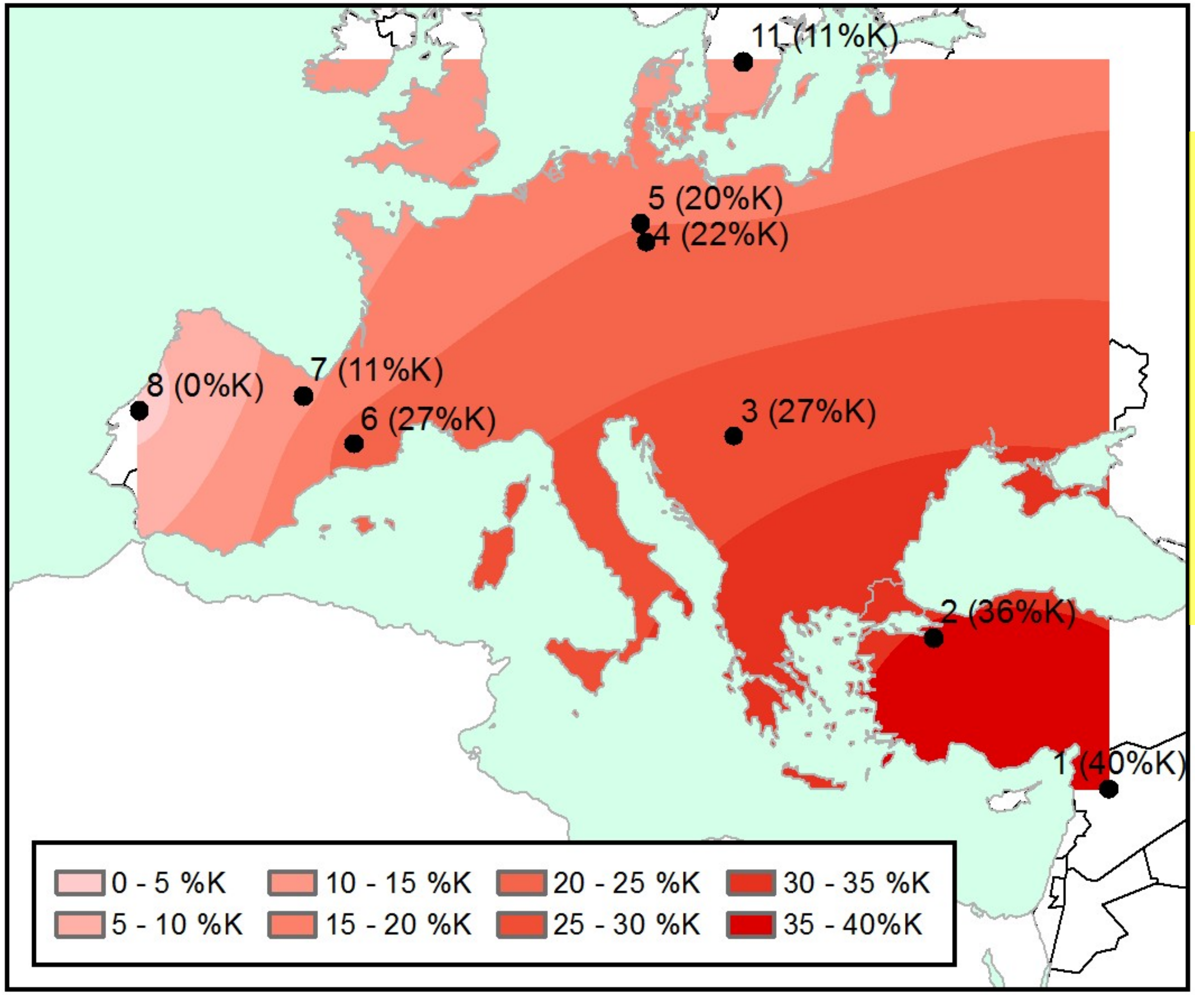
random mating for farmers→$couples\ NX = \frac{P_N P_X}{P_N+P_X}$

(3) Reproduction: each couple of farmers has 2Ro children (Ro=2.45). Genetically mixed matings (HN and NX) have 50% children N and 50% children X.

How can we compare this theory to data? Next slides

Application to the Neolithic in Europe

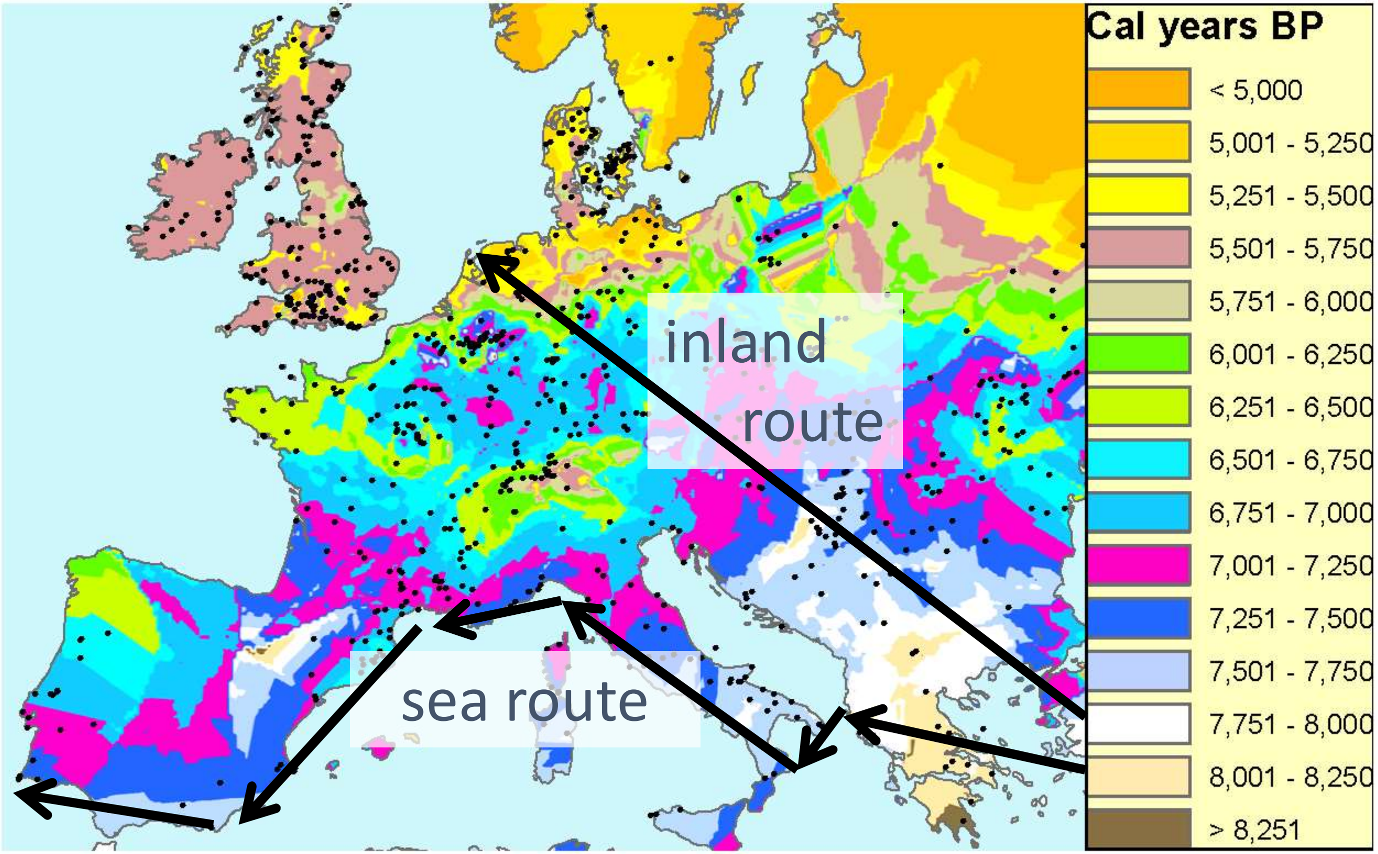
mtDNA haplogroup K: absent in hunter-gatherers



This pattern in early farmers suggests interbreeding with HGs

Isern,Fort & de Rioja, *Sci. Rep.* (2017)

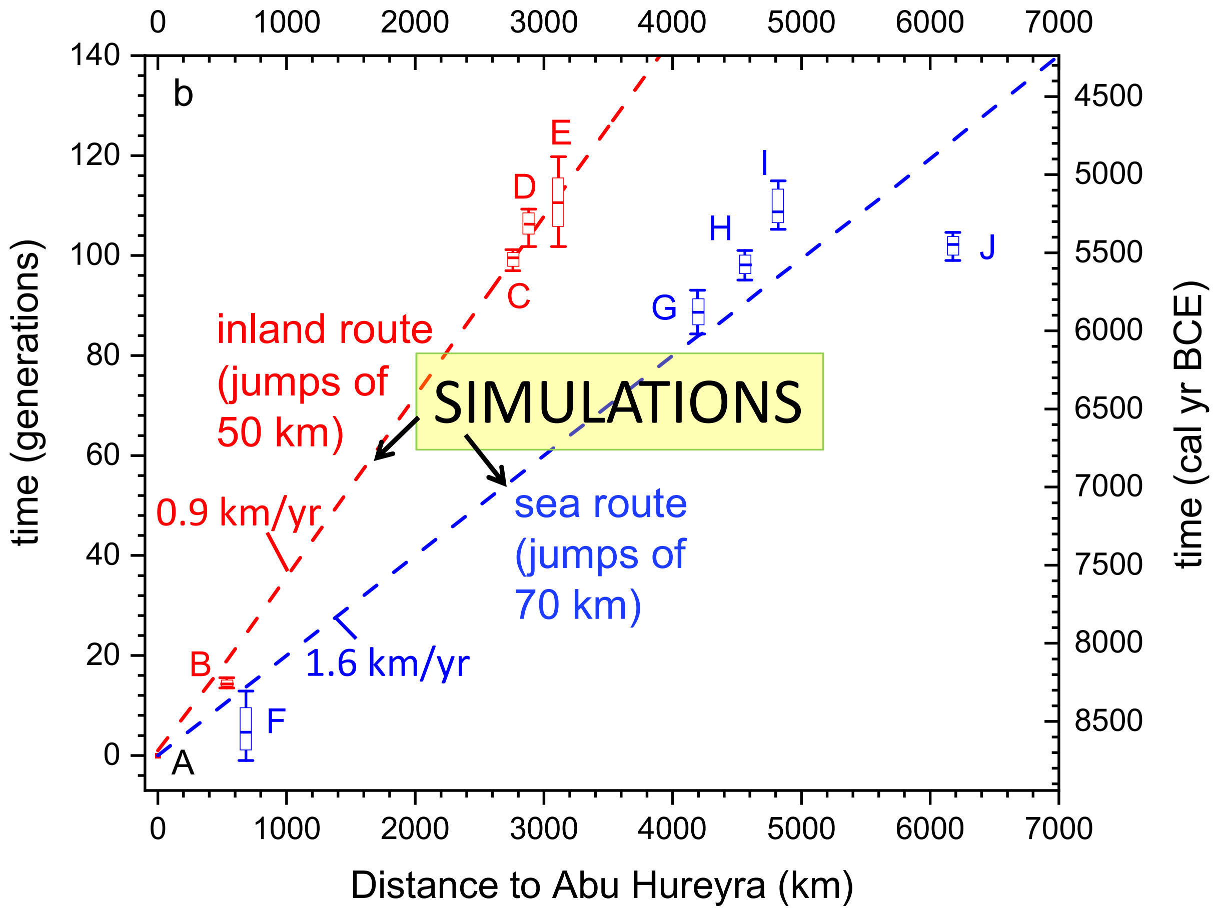
Application to the Neolithic in Europe



Now we have ancient genetic data for both routes

Application to the Neolithic in Europe

Initially there are farmers only at the cell with the **oldest PPNB site in Upper Mesopotamia (Abu Hureyra**, <9,038 cal BC) at a date (8,718 cal BC) such that the simulations agree with the data along the inland route (red).

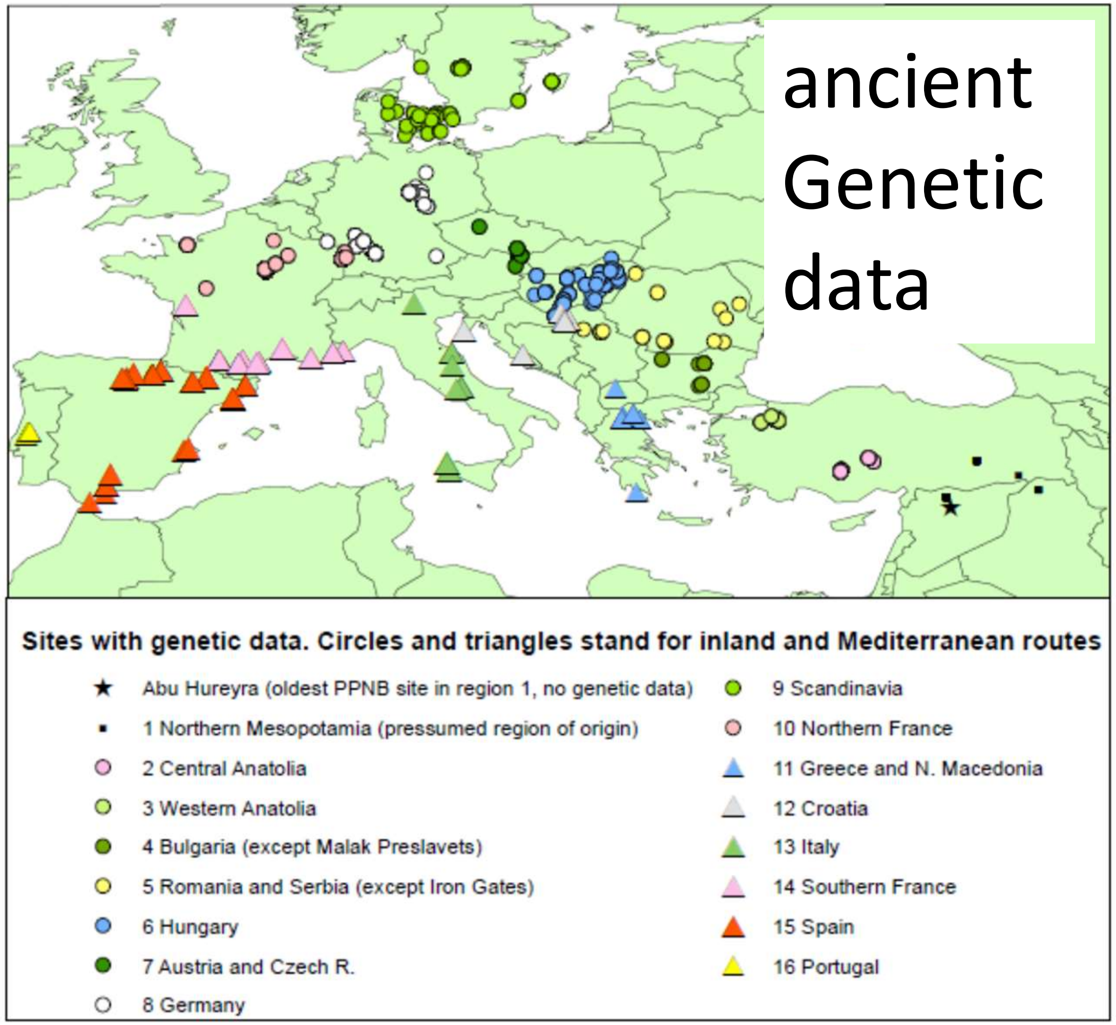


Inland route: simulations with jumps of 50 km per generation (value from ethnography)

Sea route: best fit for simulations with jumps of 70 km

Fort & Pérez-Losada, *Nature Comm.* (2024)

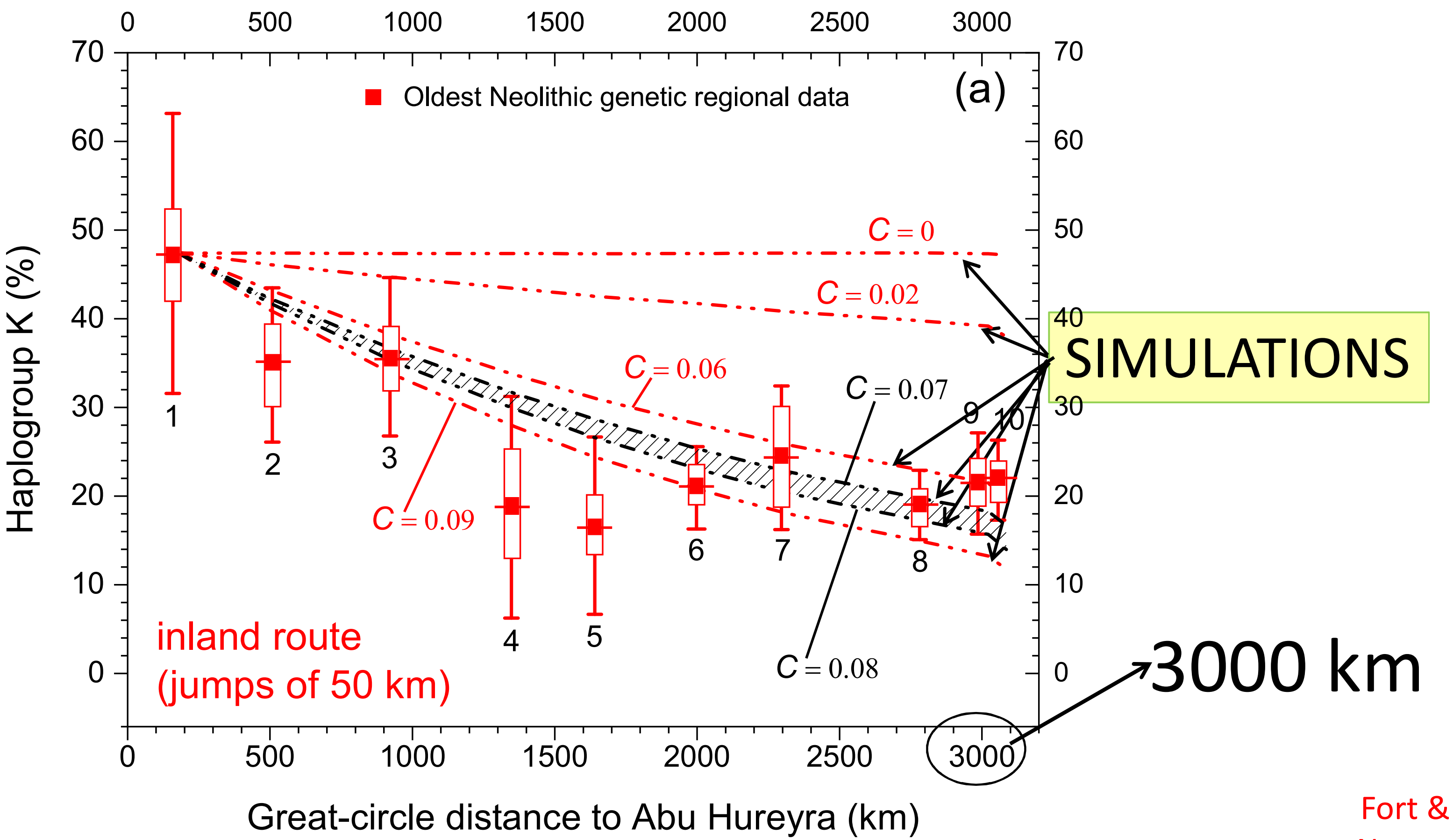
Application to the Neolithic in Europe



Fort & Pérez-Losada, *Nature Comm.* (2024)

Application to the Neolithic in Europe

Inland genetic cline

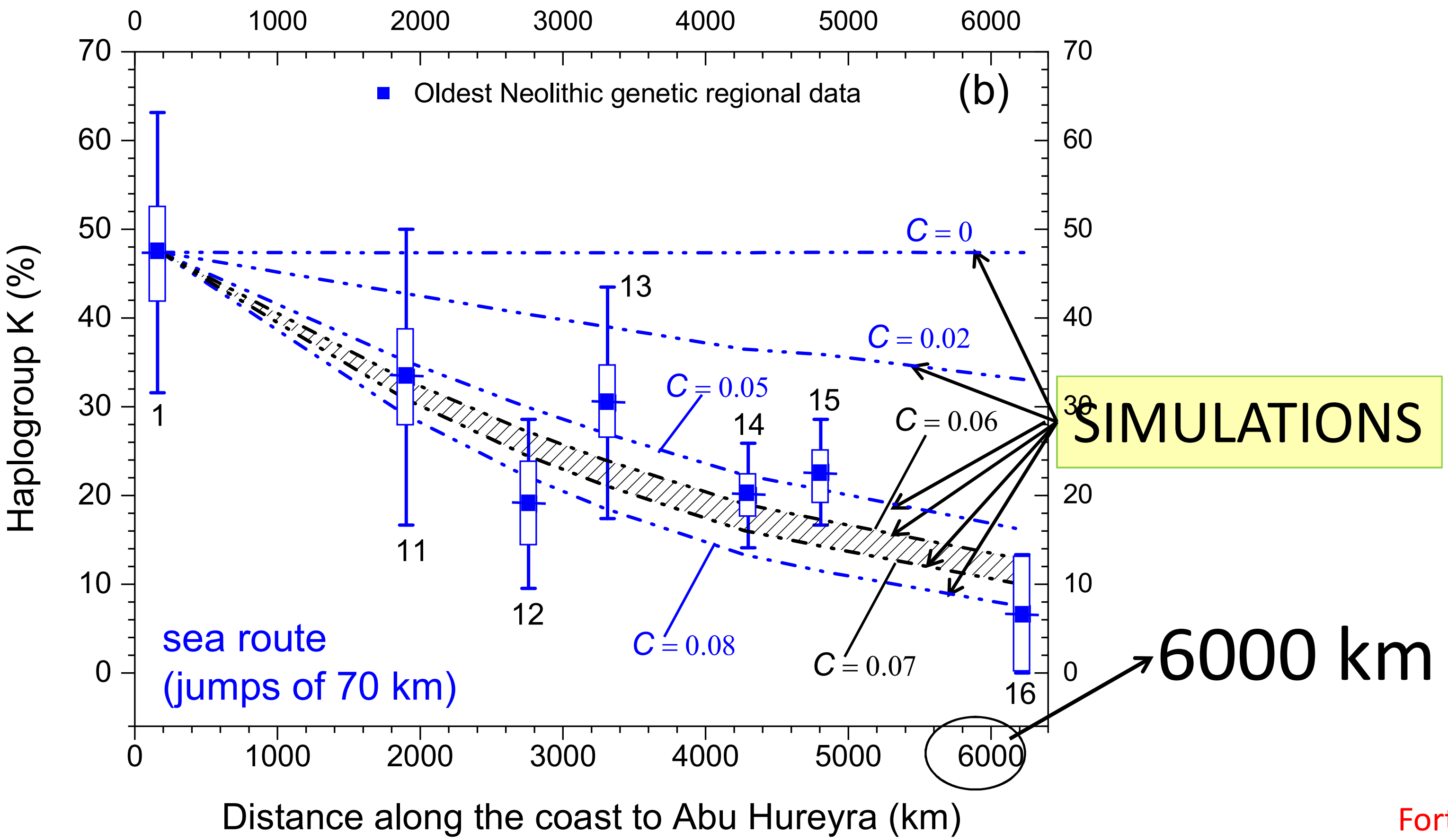


Fort & Pérez-Losada, *Nature Comm.* (2024)

Best fits: *C* = 0.07-0.08

Application to the Neolithic in Europe

Mediterranean genetic cline



Fort & Pérez-Losada, *Nature Comm.* (2024)

Best fit: *C* = 0.06-0.07.
Esentially the same as for the inland route!

Application to the Neolithic in Europe

The dispersal behavior depends on geography:
-early farmers moved longer distances per generation along the sea route.

In turn this led to:
-a faster spread rate along the sea route,
-a lower slope of the genetic cline along the sea route (due to less interbreeding events per unit distance).

In sharp contrast to this:

The number of farmers that interbred with a HG or acculturated him/her(about 3.6%* of farmers**, or *C* = 0.07***) was the same along both routes. **It did not depend on geography but only on the transition in the subsistence economy and its associated way of life.**

*fraction of farmers = $\frac{P_F(x,y,t+1) - P_F(x,y,t)}{P_F(x,y,t)} = C \frac{P_{HG}(x,y,t)}{P_{HG}(x,y,t) + P_F(x,y,t)} = \frac{100\,C}{1 + \frac{p_{F\,min}}{p_{HG\,max}}}$

Application to the Neolithic in Europe

UNCERTAINTIES:

·previous slides: about **3.6%** of farmers interbred with a HG or acculturated him/her ($\boldsymbol{C \approx 0.07}$).

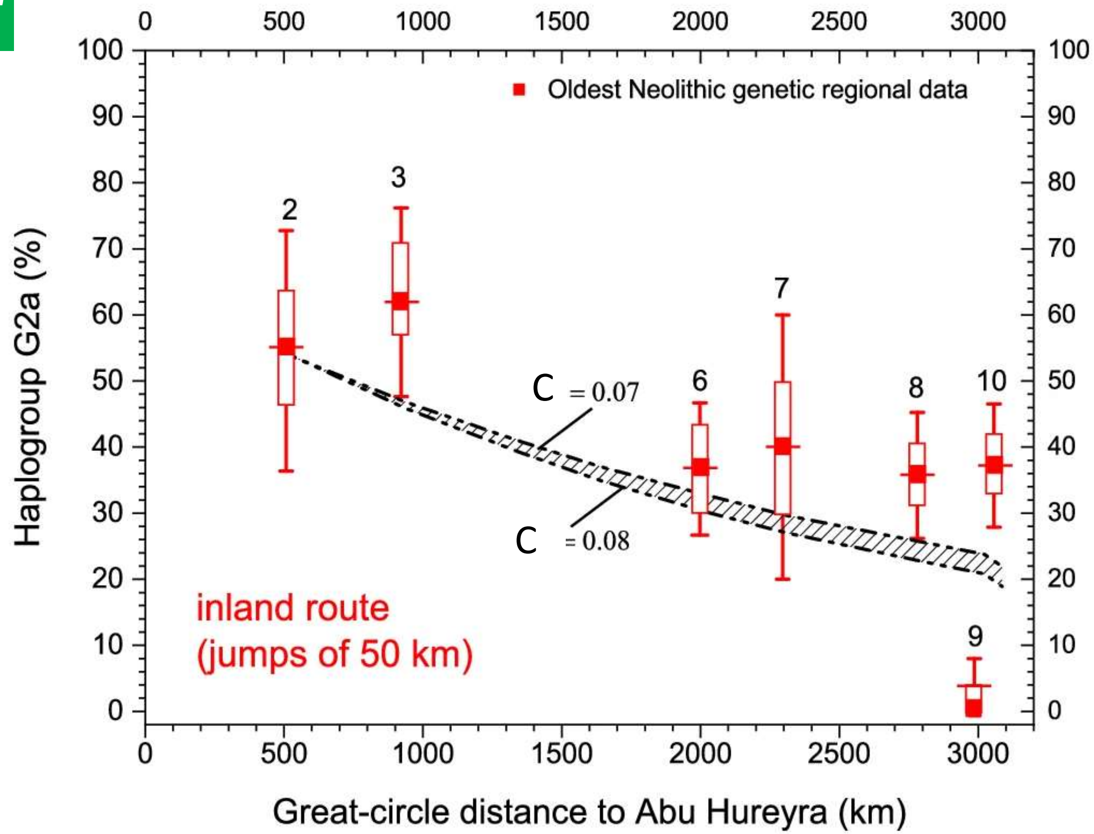
·Taking into account the uncertainties in the parameter values ($p_{F\,max}$, $p_{HG\,max}$, $p_{F\,min}$, R_0) and in the initial frequencies of haplogroup K: **1% - 8%** of farmers interbred with a HG or acculturated him/her ($\boldsymbol{0.03 < C < 0.14}$).

Fort & Pérez-Losada, *Nature Comm.* (2024)

Application to the Neolithic in Europe

Y chromosome

Haplogroup G2 is the most frequent one in farmers.
It is essentially absent in hunter-gatherers



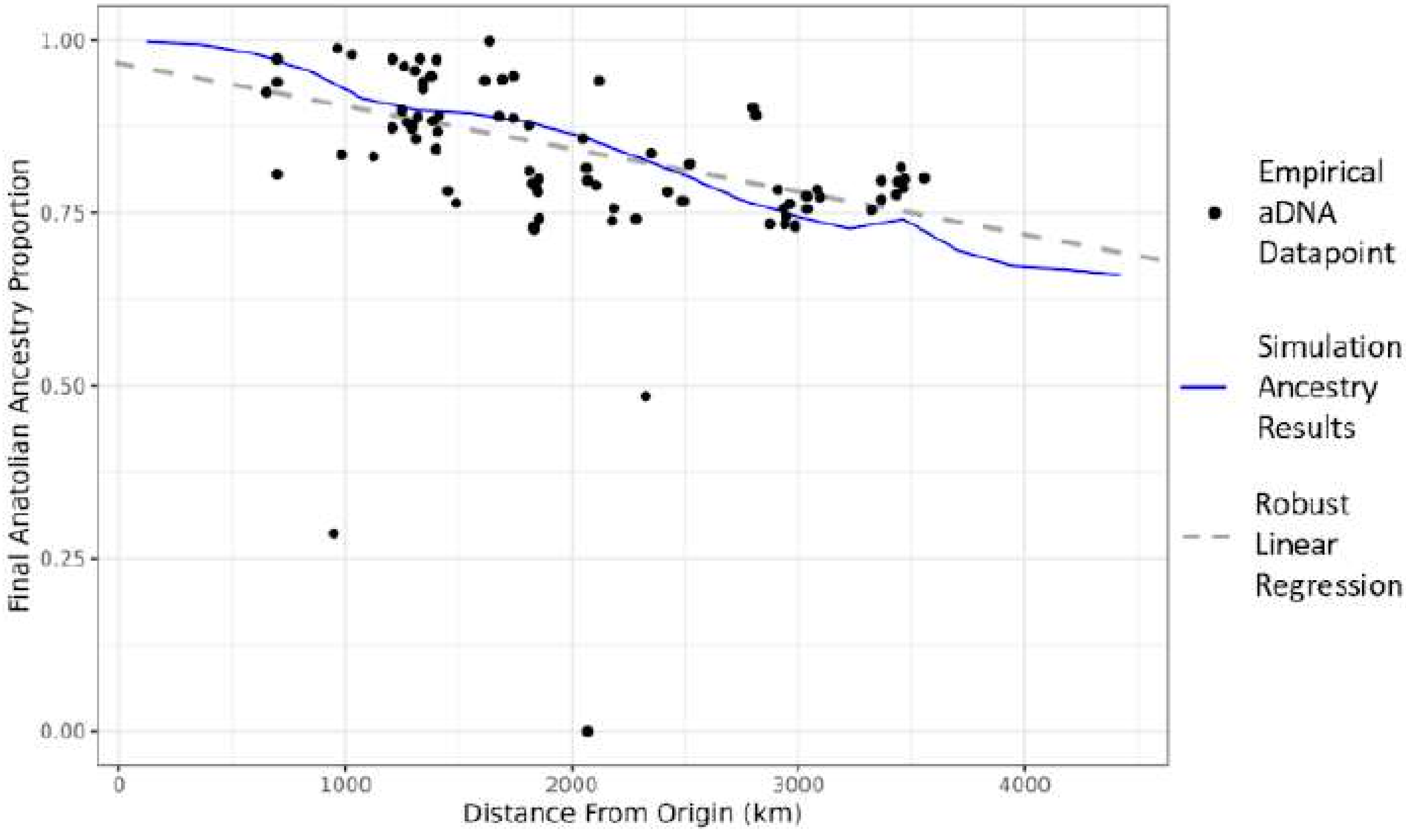
We obtain again *C ≈ 0.07*, in agreement with the mt DNA results

Fort & Pérez-Losada, *Nature Comm.* 2024

For the sea route there are not enough data

Application to the Neolithic in Europe

Whole genome

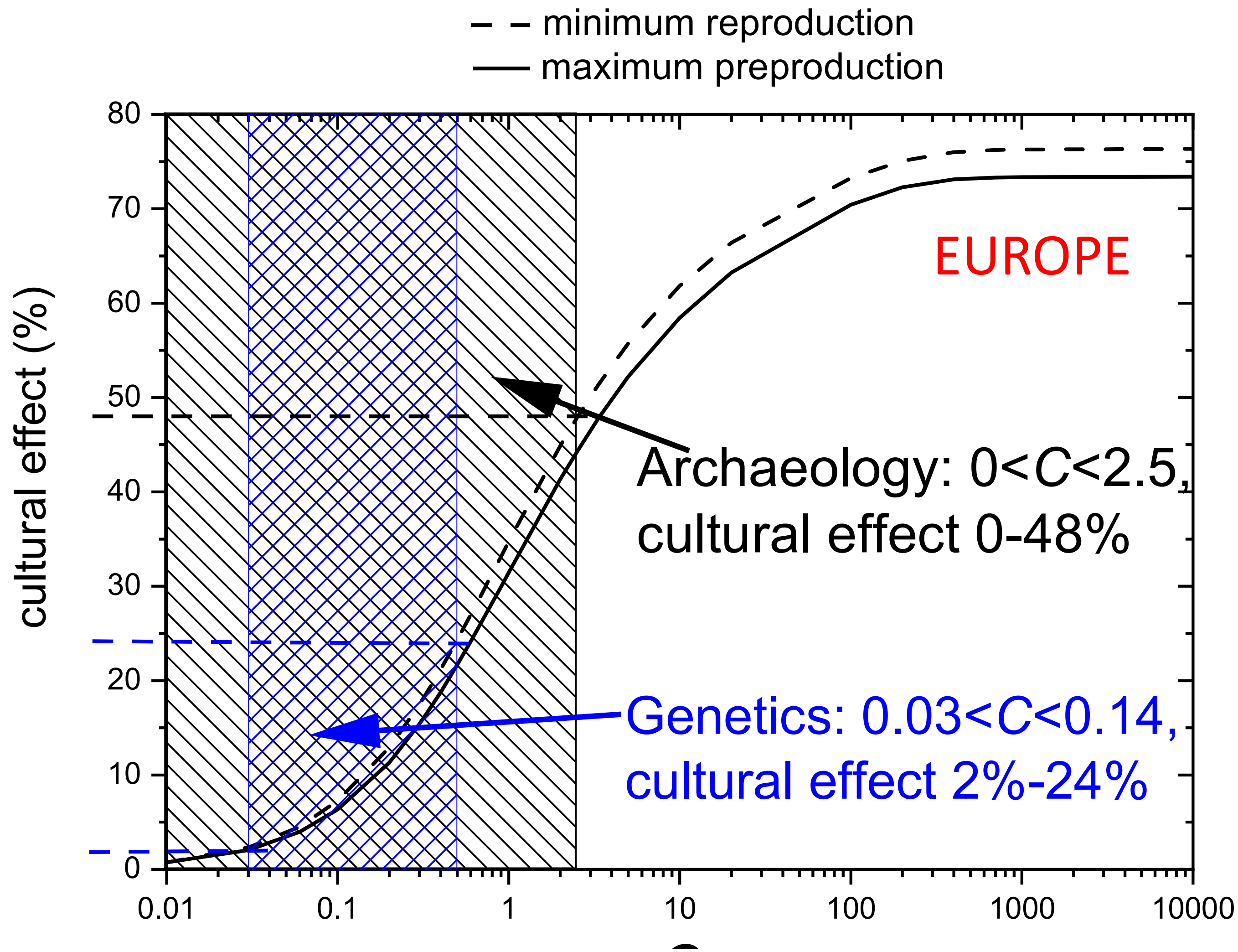


LaPolice, Williams & Huber, bioRxiv (2024)

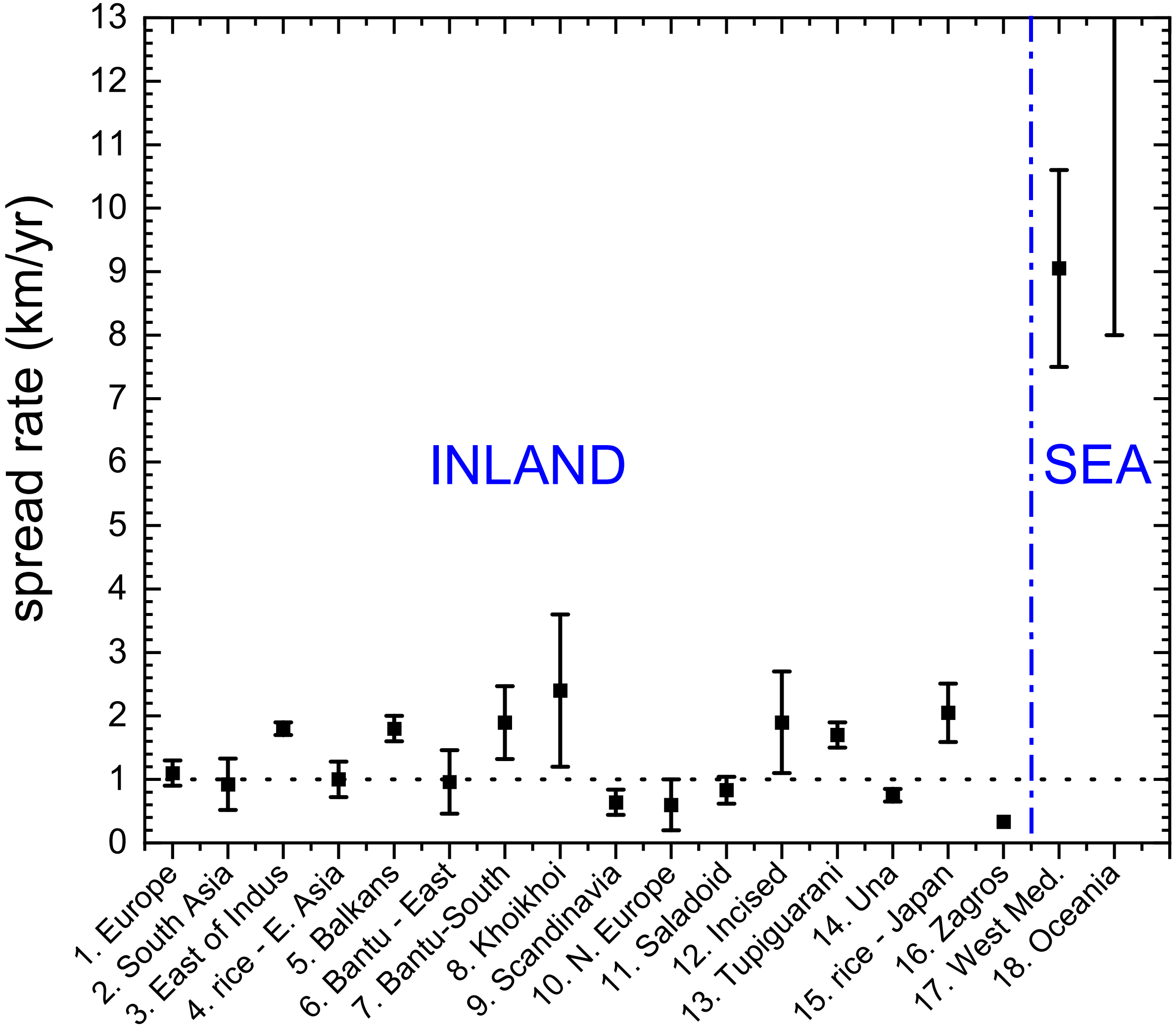
They obtain that about 0.1% of early farmers interbred with a HG or acculturated him/her each year, i.e. about 0.1% ·32 yr = 3.2% per generation.
This is consistent with our estimation (previous slides) of 3.6% (more precisely 1% - 8%).

Application to the Neolithic in Europe

We go back to a figure obtained in a previous slide from Archaeology (black):

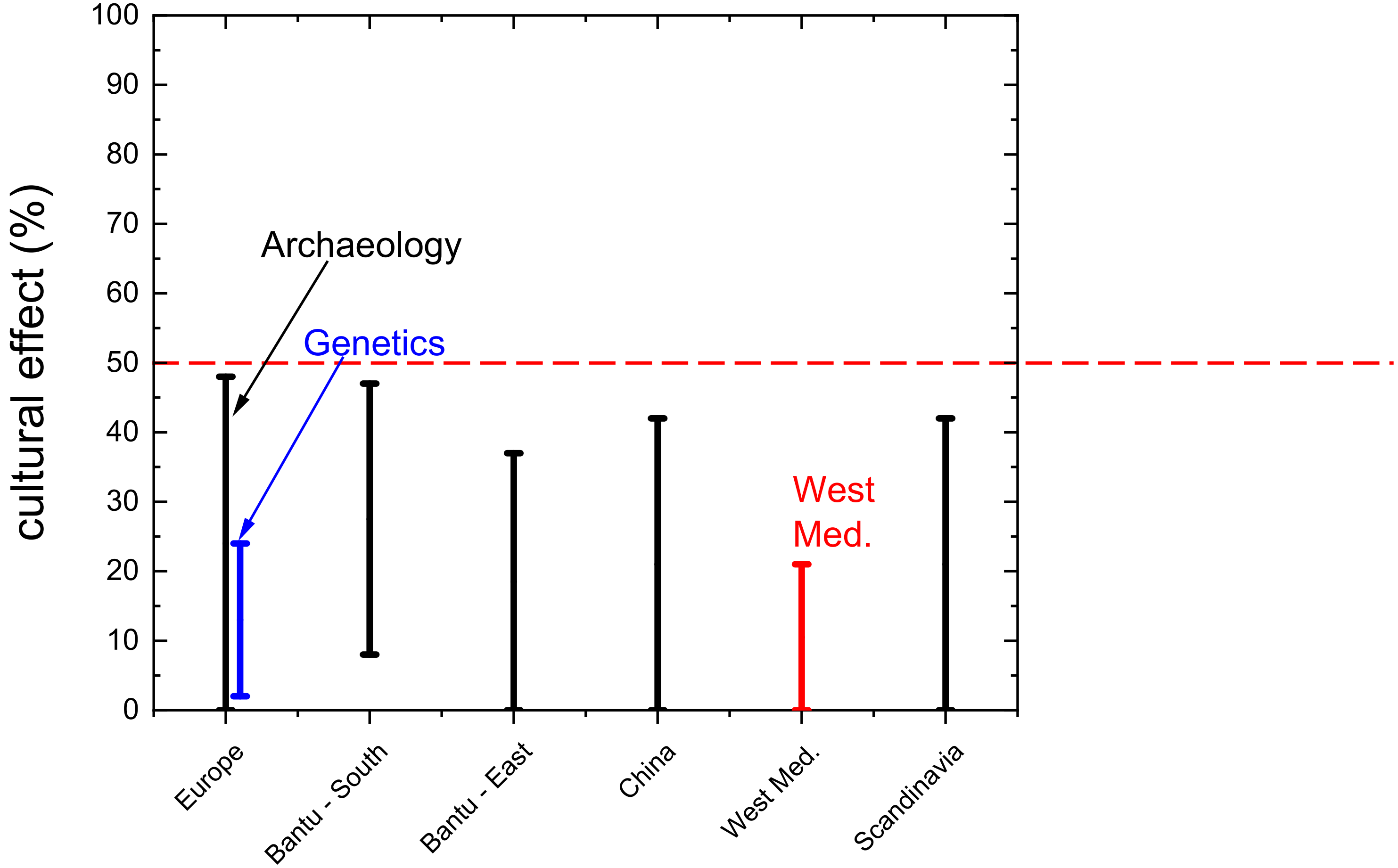


Prehistoric dispersals of farming and herding



J. Fort, Tendencies in the tempo of pre-modern expansions. Submitted (2024)

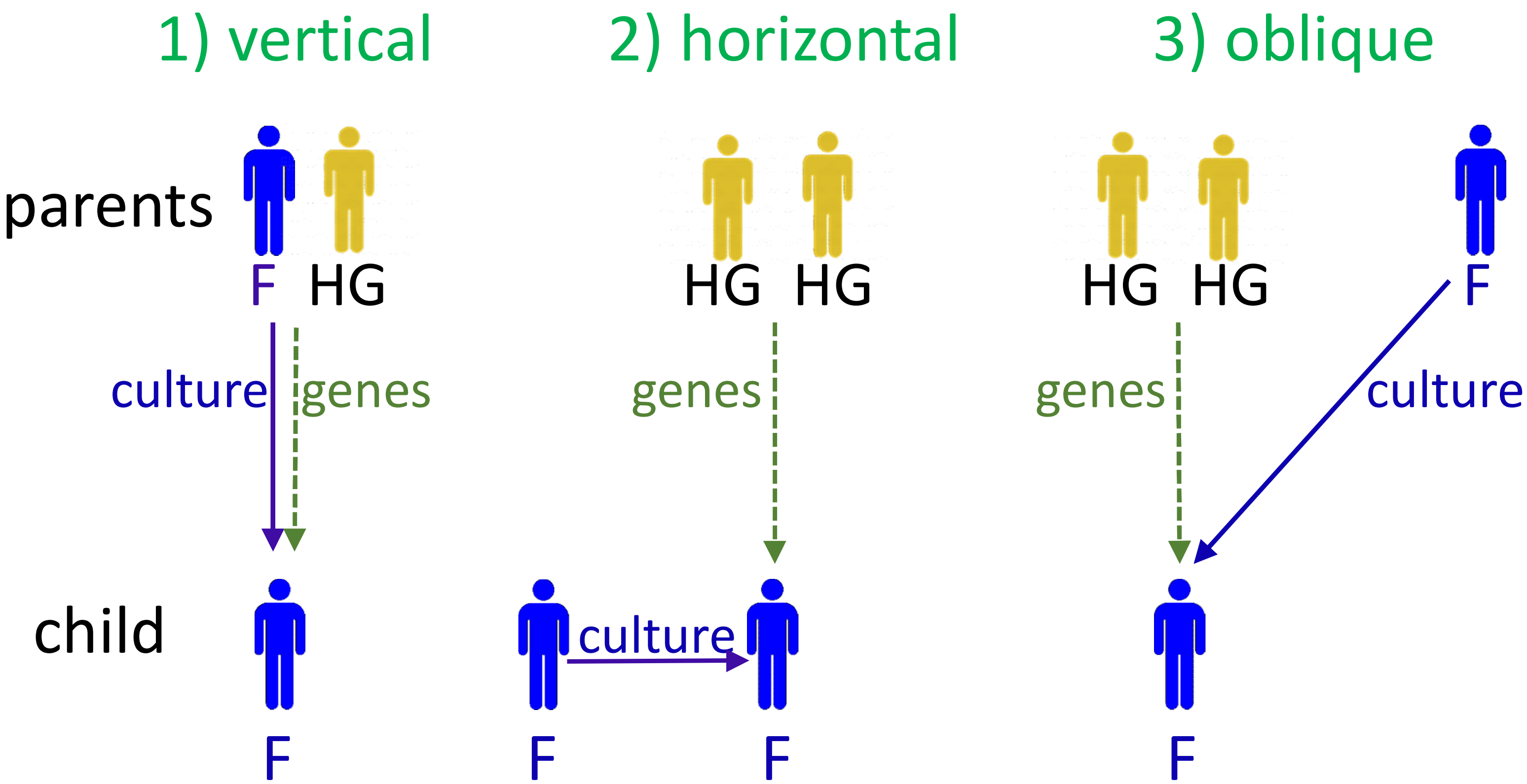
Prehistoric dispersals of farming and herding



J. Fort, The spread of agriculture: general laws in prehistory? *in Simulating transitions to agriculture in prehistory,* eds. S. Pardo-Gordó & S. Bergin (Springer, Cham, 2021), p. 17-28.

Cultural transmission

3 types



Oblique cultural transmission

Infantile HGs learn farming from **adult** farmers, so **we need 4 populations** with densities (number of people/km^2):

Infantile farmers: $p_I(x, y, t)$
Adult farmers: $p_A(x, y, t)$

Infantile HGs: $q_I(x, y, t)$
Adult HGs: $q_A(x, y, t)$

Oblique cultural transmission

First a simple model without cultural transmission (only farmers):

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

where

· F = fecundity = number of children born per adult during τ, and still alive at *t*=τ.

Thus (1) → p_I (infantiles) are aged 0- τ; p_A (adults) are aged above τ.

· m_I = infantile mortality=portion of individuals aged 0-τ at *t* and died at *t*+τ.

· m_A = adult mortality=portion of individuals aged above τ at *t* and died at *t*+τ.

· τ ≈16 yr is suggested by ethnographic data (start of reproduction).

· $\phi\left(\Delta_x, \Delta_y\right)$=dispersal kernel: Again a portion p_e (persistency) do not migrate, the rest move isotropically a distance *r*.

Fort, *Chaos, Solitons & Fractals* (2021)

Oblique cultural transmission

We add oblique transmission between adult farmers p_A and infantile HGs q_I:

Fort, *Chaos, Solitons & Fractals* (2021)

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

Infantile HGs learn skills until about 16 yr [1]

[1] Hewlett & Cavalli-Sforza, Cultural transmission among Aka pygmies. *Amer. Anthropol.* 1986

Oblique cultural transmission

$$\text{speed}= \min_{\lambda > 0} \frac{\ln \quad {}_1(\lambda)}{\lambda\tau} \quad [1]$$

where $\rho_1(\lambda)$ is the largest of the eigenvalues of the linearized matrix M.

In our case this yields [2]: $$\text{speed}= \min_{\lambda > 0} \frac{\ln\frac{(1-m_I)\,C\,f(\lambda r)+(1-m_A)+\sqrt{[(1-m_I)\,C\,f(\lambda r)+(1-m_A)]^2+4F(1-m_I)\,f(\lambda r}}{2}}{\lambda\tau}$$

where $C = \frac{f}{\gamma}$,

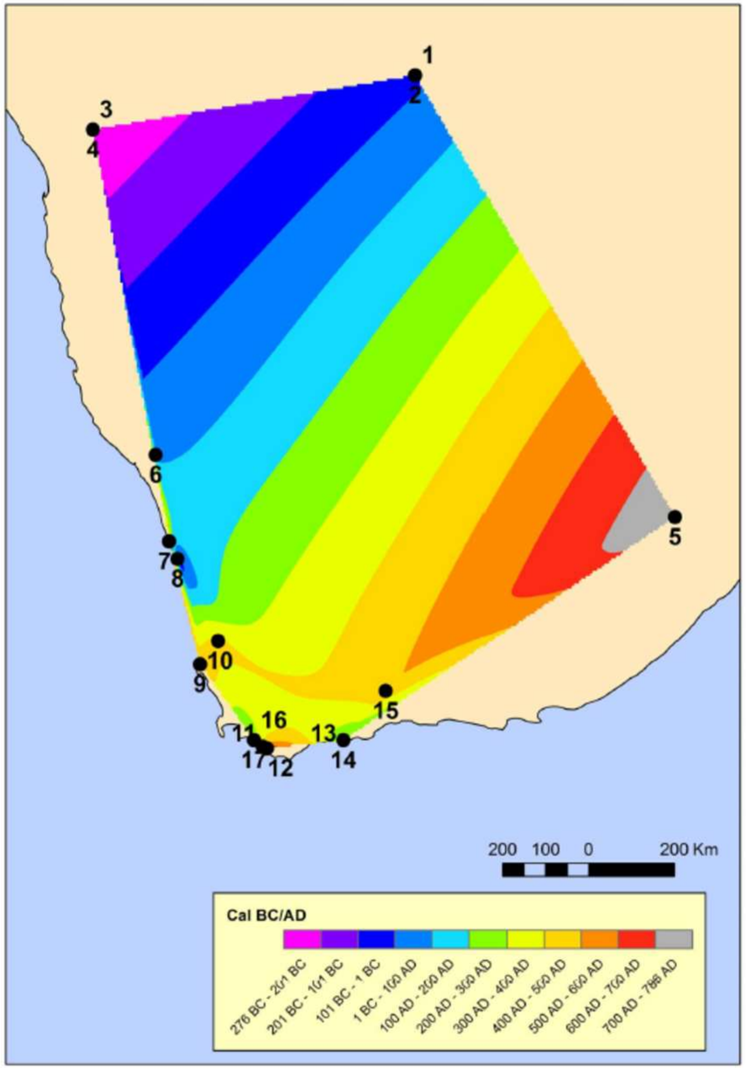
$f(\lambda r) = p_e + (1 - p_e)I_0(\lambda r),$

$I_0(\lambda r) = \frac{1}{2\pi}\int_0^{\infty} d\theta \exp[\lambda\, r\, cos\theta]$=modified Bessel function of the first kind and order zero

[1] Neubert, M. & Caswell, H. “Demography and Dispersal: Calculation and sensitivity analysis of invasion speed for structured populations," *Ecology* (2000)

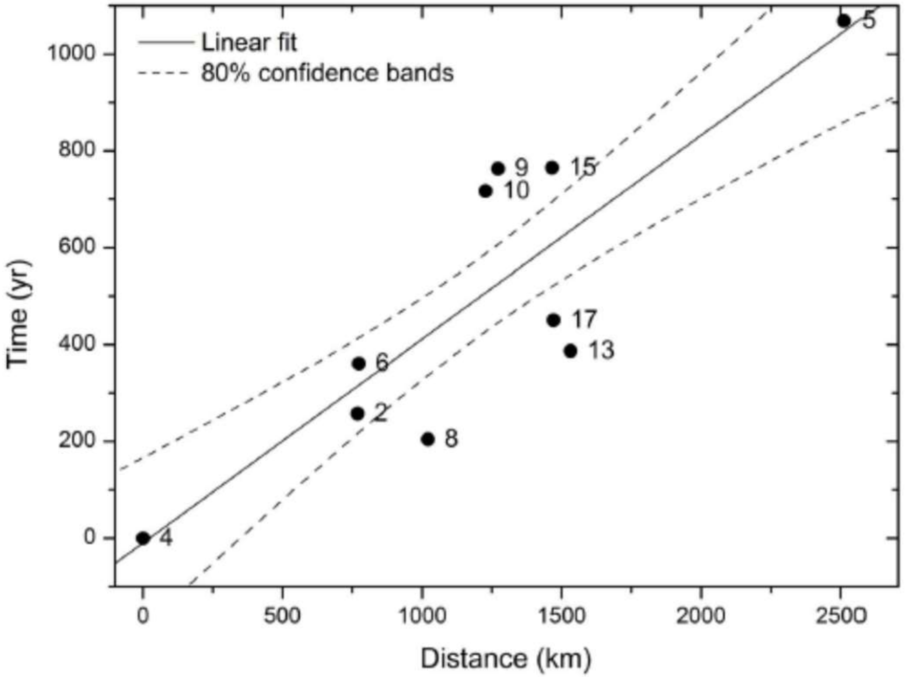
[2] Fort, J. “Front propagation and cultural transmission. Theory and application to Neolithic transitions.” *Chaos, Solitons & Fractals* (2021)

Oblique cultural transmission



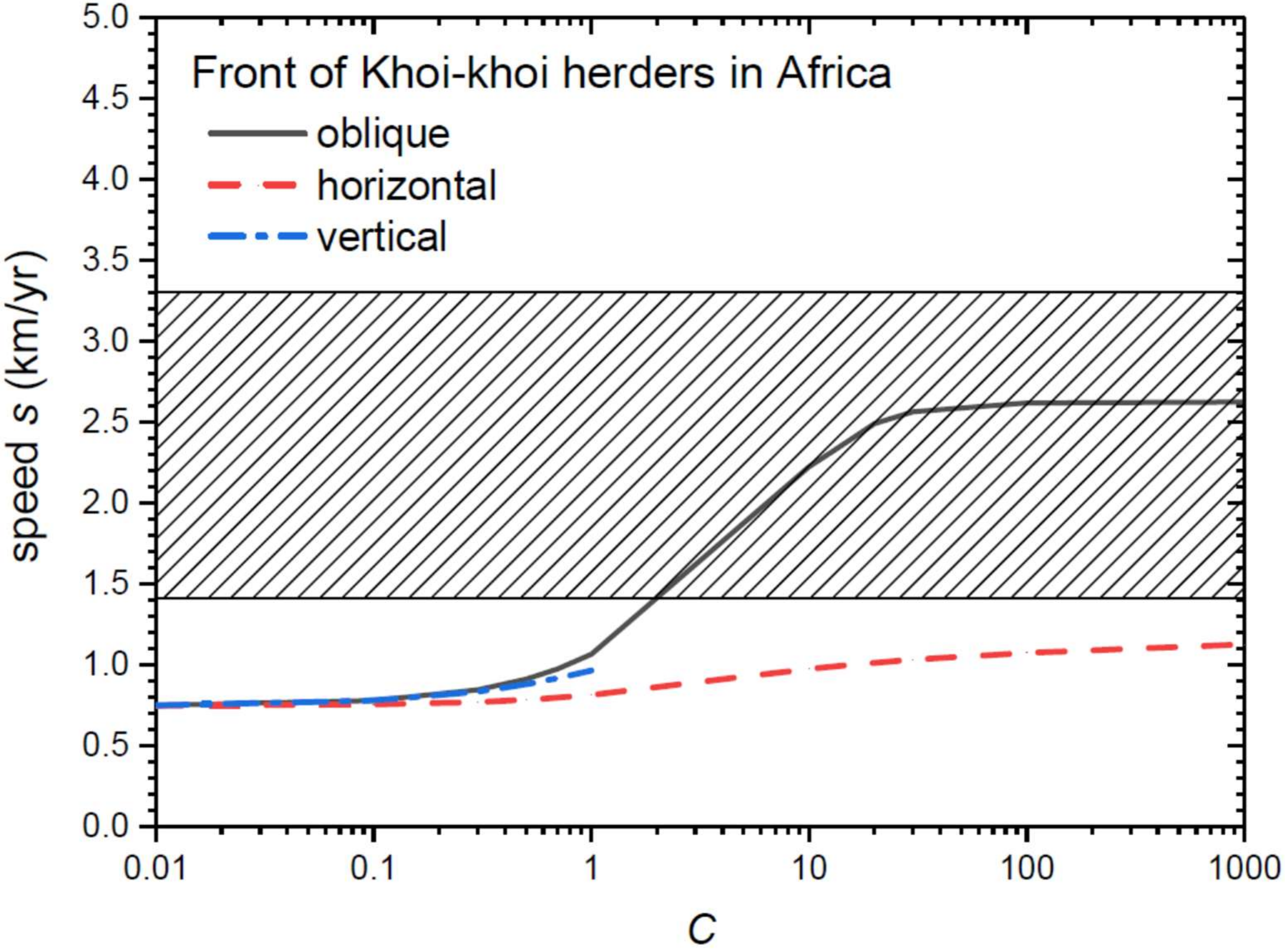
Expansion of Khoi-khoi
herders (not farmers) in southwestern Africa.

speed = 1.4-3.3 km/yr.



Jerardino, Fort, Isern & Rondelli, PLoS One (2014)

Oblique cultural transmission



Parameter values for pre-industrial herders (not farmers), from ethnography:
$p_e = 0.67, r = 42$ km, $m_A = 0.49, m_I = 0.29$, $F = 2.69$ and $\tau = 16$ yr

Fort, *Chaos, Solitons & Fractals* (2021)

Oblique cultural transmission

Conclusions

·Oblique transmission leads to faster fronts than vertical and horizontal transmission (as expected intuitively).

·Fast range expansions (e.g., that of Khoi-khoi herders) can be explained by oblique transmission but apparently not by vertical neither horizontal transmission.

Fort, *Chaos, Solitons & Fractals* (2021)