Demic-cultural models, archaeology and genetics of Neolithic spread

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The Neolithic transition is the shift from hunting-gathering into farming (and/or herding).
Farming (i.e., the Neolithic) appeared in different places and times.
It spread gradually across several huge regions.

Reaction-diffusion range expansion models attempt to understand the speed of such spreads, the mechanisms driving them, and their genetic consequences.

Models of Neolithic spread

- **Demic diffusion** = spread of farming populations = dispersal + net reproduction
- **Cultural diffusion** = spread of ideas = incorporation of hunter-gatherers into farming populations, via either transmission of plants, animals and knowledge from farmers to HGs(acculturation) and/or via interbreeding between HGs and farmers.
- **Demic-cultural models**

PLAN OF THE TALK

FIRST PART: mathematical models

1. reaction-diffusion *vs* reaction-dispersal
2. non-cohabitation *vs* cohabitation eqs.
3. cultural transmission *vs* Lotka-Volterra eqs.

SECOND PART: comparison to data

4. Archaeology (Europe, Asia, Africa)
5. Genetics (Europe)

1. reaction-diffusion *vs* reaction-dispersal

Fisher's equation

$$\frac{\partial F}{\partial t} = D_F \nabla^2 F + a_F F \left(1 - \frac{F}{K_F}\right)$$

$F = F(x,y,t)$ = population density (e.g., farmers)

D_F = diffusion coefficient

Logistic growth:

a_F = initial growth rate

K_F = carrying capacity

speed of range expansions = $\sqrt{2 a_F D_F}$

Derivation of Fisher's equation

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

T = generation time

$\phi_F(\Delta_x,\Delta_y)$= probability to move (Δ_x,Δ_y) during T

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

A Taylor expansion ($\Delta_x \approx 0$, $\Delta_y \approx 0$, $T \approx 0$) yields Fisher's eq., with $D_F = \frac{\overline{\Delta^2}}{4T}$.

Fort & Méndez, Phys. Rev. Lett. (1999)

Is Fisher's eq. a good approximation <u>for humans</u>?

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

$$\text{speed} = \min_{\lambda > 0} \frac{\ln\left[\left(e^{a_F T}-1\right)\sum_{j=1}^{M} p_j\, I_0(\lambda r_j)\right]}{T\lambda},$$

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

We will compare this speed to Fisher's = $\sqrt{2a_F D_F}$

Preindustrial populations (farmers)

Population A*: $\{p_j\}$={0.54, 0.17, 0.04, 0.25},

$\{r_j\}$={2.4, 14.5, 36.3, 60.4}km.

Population B*: $\{p_j\}$={0.40, 0.17, 0.17, 0.26},

$\{r_j\}$={2.4, 14.5, 36.3, 60.4}km.

Population C*: $\{p_j\}$={0.19, 0.07, 0.22, 0.52},

$\{r_j\}$={2.4, 14.5, 36.2, 60.4}km.

Population D**: $\{p_j\}$={0.19, 0.54, 0.17, 0.04, 0.04, 0.02},

$\{r_j\}$={5, 30, 50, 70, 90, 110}km.

Population E***: $\{p_j\}$={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.

*Ethiopia; **Brazil; ***Central African Republic

Preindustrial populations (farmers)

Values of a_F and T:

$0.023\ y^{-1} \leq a_F \leq 0.033\ y^{-1}$ (from 4 ethnographic and 1 archaeological populations)

$T = 32\ y$ (from ethnographic data)

Population	speed (km/yr)	Fisher (km/yr)	error Fisher
A	0.71-0.81	0.85-1.02	20%-26%
B	0.75-0.84	0.93-1.11	24%-32%
C	0.92-1.01	1.26-1.51	37%-**50%**
D	0.93-1.06	1.11-1.34	19%-26%
E	0.61-0.74	0.54-0.65	-11%--12%

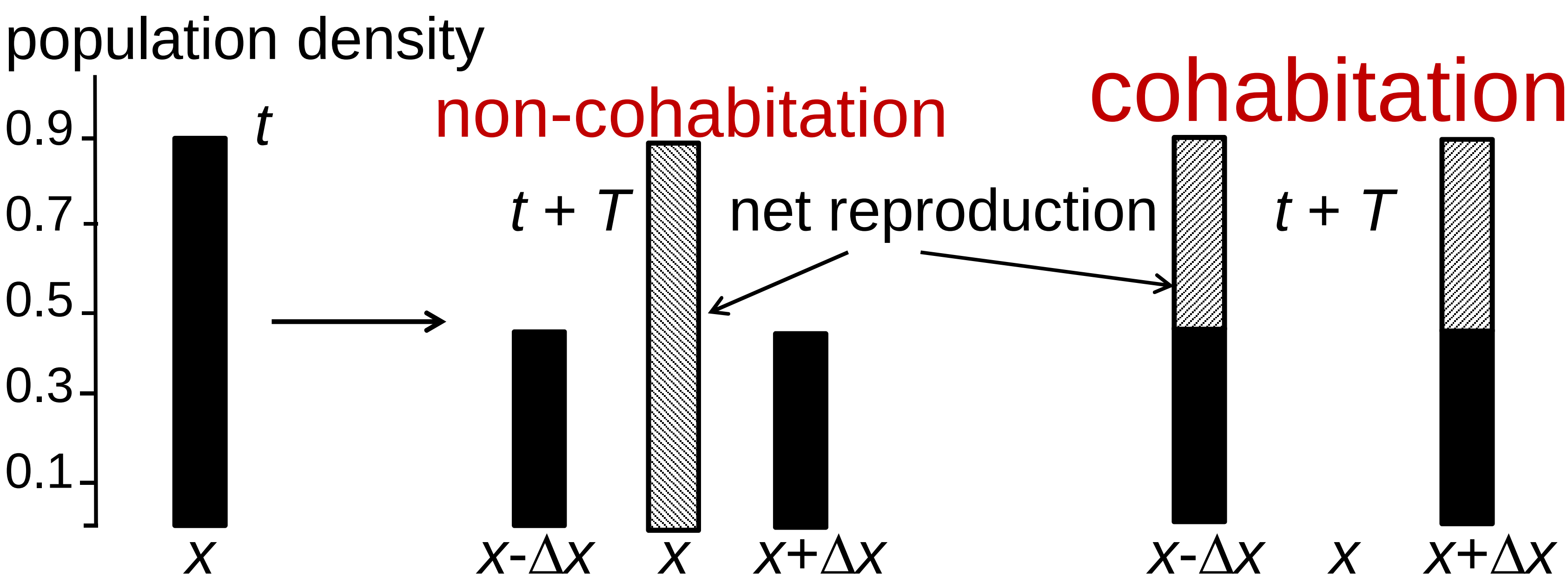
Isern, Fort & Pérez-Losada, JSTAT (2008)

2. non-cohabitation *vs* cohabitation eqs.

Up to now: non-cohabitation eq.: $F(x,y,t+T) - F(x,y,t) = \int_{-\infty}^{\infty}\int_{-\infty}^{\infty} F(x+\Delta_x, y+\Delta_y, t)\ \phi_F(\Delta_x,\Delta_y)\, d\Delta_x\, d\Delta_y - F(x,y,t) + R_T[F(x,y,t)] - F(x,y,t)$

Cohabitation equation:

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



Preindustrial populations (farmers)

Population	Cohabitation (km/yr)	**error non-cohab. (relative to cohab.)**	error Fisher (relative to cohab.)
A	0.91-1.10	-22%--26%	-6%--8%
B	0.96-1.15	-22%--27%	-5%--3%
C	1.20-1.40	-23%--**28%**	5%-8%
D	1.18-1.44	-21%--26%	-6%--7%
E	0.74-0.94	-18%--22%	27-**31%**

Another way to see the limitations of Fishers' eq.:

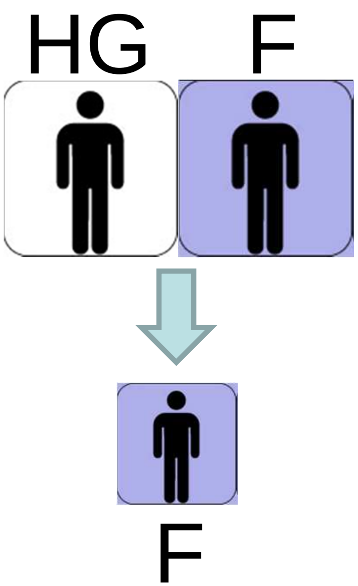
Fisher's speed = $\sqrt{2a_F D_F} \rightarrow \infty$ if $a_F \rightarrow \infty$

Cohabitation speed* $\rightarrow \frac{r_{max}}{T}$ if $a_F \rightarrow \infty$

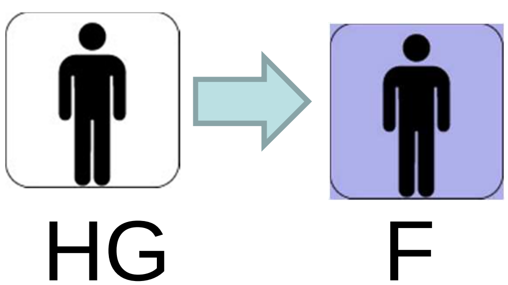
$$* \text{ cohabitation speed} = \min_{\lambda > 0} \frac{a_F T + \ln\left[\sum_{j=1}^{M} p_j I_0(\lambda r_j)\right]}{T\lambda}$$

3. cultural transmission *vs* Lotka-Volterra eqs.

Cultural transmission takes 2 forms:



1) **Vertical** = due to interbreeding between hunter-gatherers (HG) and farmers (F)



2) **Horizontal/oblique** = due to acculturation (teaching and/or copying)

Cultural transmission

Are Lotka-Volterra equations adequate?

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

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

Problem:

Number of HGs converted per farmer according

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

if $P_H \rightarrow \infty$

Cavalli-Sforza & Feldman, *Cultural transmission and evolution* (1981), p.131 & 151 (oblique & horiz. trans.)

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

[If n were proportional to $P_F + P_H$, we would obtain L-V eqs.]

[But n is roughly the same for many populations (Dunbar, 1993).]

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

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

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

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

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

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

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

per generation

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

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

Number of HGs converted per farmer:

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

$$\text{if } P_H \to \infty$$

<u>There is a maximum</u>.

These equations are different from Lotka-Volterra eqs.:

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

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

<u>No maximum</u>.

$$\text{if } P_H \to \infty$$

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

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

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!

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 proportion ρ of his F neighbors and a proportion κ of his HG neighbors, then:

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

$\gamma = \kappa/\rho$

Then:

if $P_F \gg P_H$

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

$$P_H' = P_H - f\frac{P_F P_H}{P_F+\gamma P_H} \approx P_H + \frac{f}{\gamma}\,P_F \rightarrow \frac{P_H - P_H'}{P_F} = \frac{f}{\gamma}\text{ not} \leq 1$$

if $P_H \gg P_F$

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

$$\begin{cases} \text{farmers } (F)\text{:} \quad P'_F = P_F + f\,\dfrac{P_F P_H}{P_F + \gamma P_H} \\ \text{hunter} - \text{gatherers } (H)\text{:} \quad P'_H = P_H - f\,\dfrac{P_F P_H}{P_F + \gamma P_H} \end{cases}$$

$\gamma < 1$ indicates preference of *H*s to copy *F*s rather than *H*s

If $\gamma \approx 1$: random copying

Frequency-dependent transmission yields more complicated eqs. and a slower front speed, but the same speed as a function of a parameter that can be called the cultural transmission intensity*

*Fort, *PNAS* 2012

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

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

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

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

$C = \dfrac{P_H' - P_H}{P_F}$ = number of HGs converted per F per generation (in horizontal and/or obique transmission)

or

$C = \dfrac{P_F' - P_F}{P_F}$ = fraction of Fs that mate HGs per generation

(in vertical transmission*→$\gamma = 1$ and $C \leq 1$;
if $f = 1$: random mating)

* Fort, Phys Rev E 2011

Using population densities (*F* = farmers, *H* =HGs)

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

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

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

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

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

Fort, *PNAS* 2012

Demic-cultural models

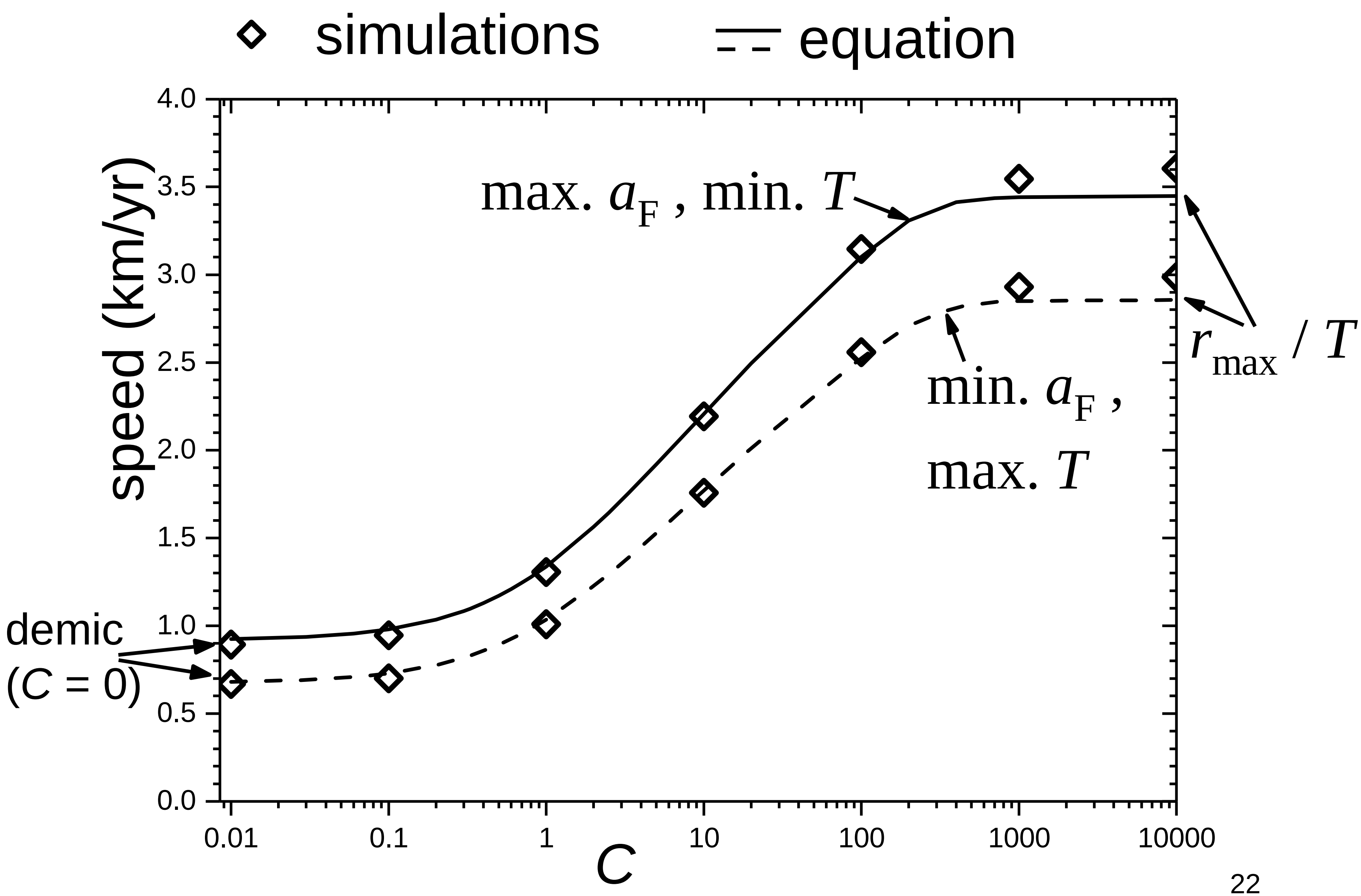
The front speed for the previous set is

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

Without cultural transmission (C=0), we recover the speed of the cohabitation single-population model (given in a previous slide).

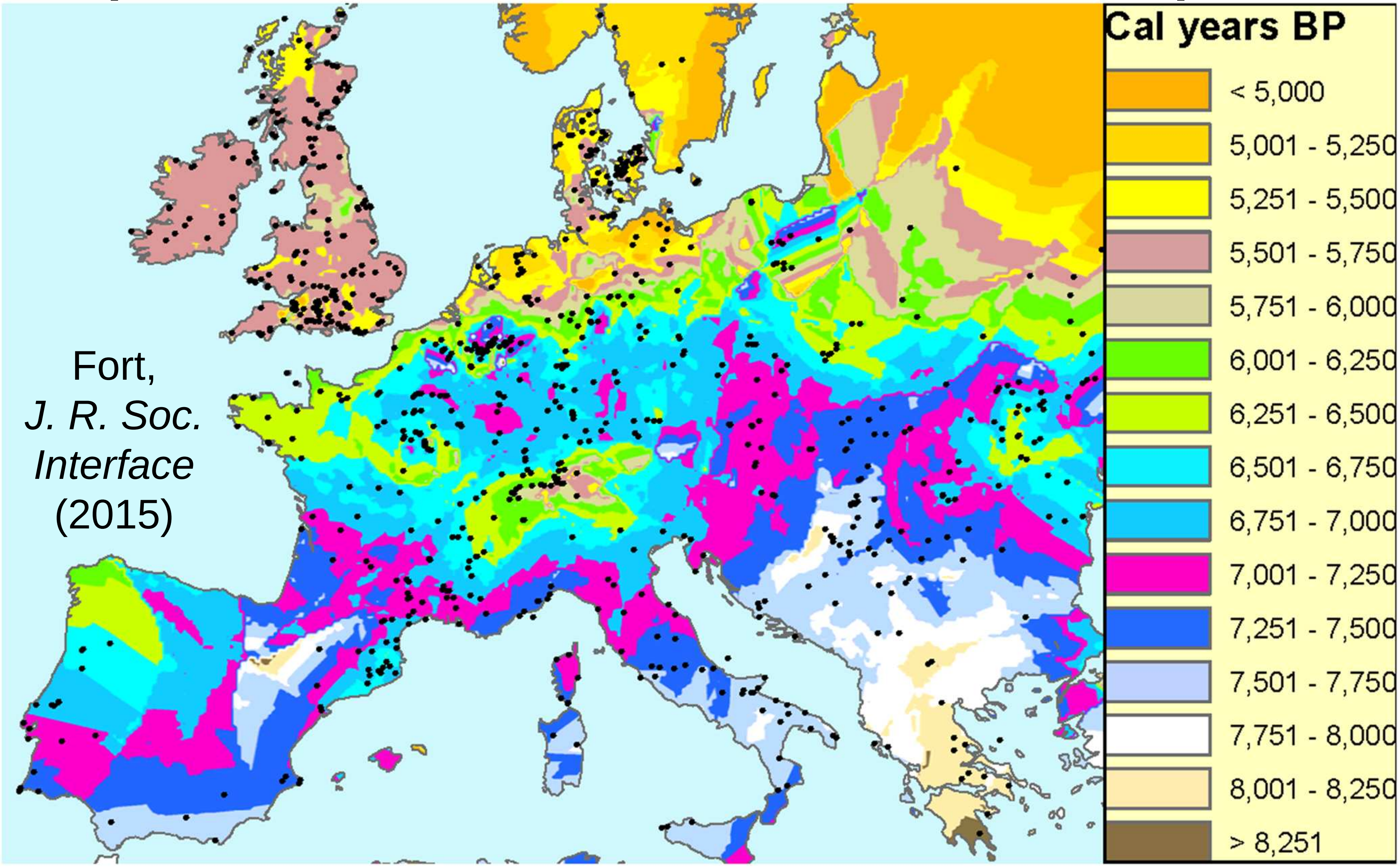
More general models include, besides besides the demic disperal kernel $\{p_j, r_j\}$, a cultural dispersal kernel $\{P_j, R_j\}$ (Fort, *JRS Interface* 2015)

Plot of the front speed using the Eq. in the previous slide



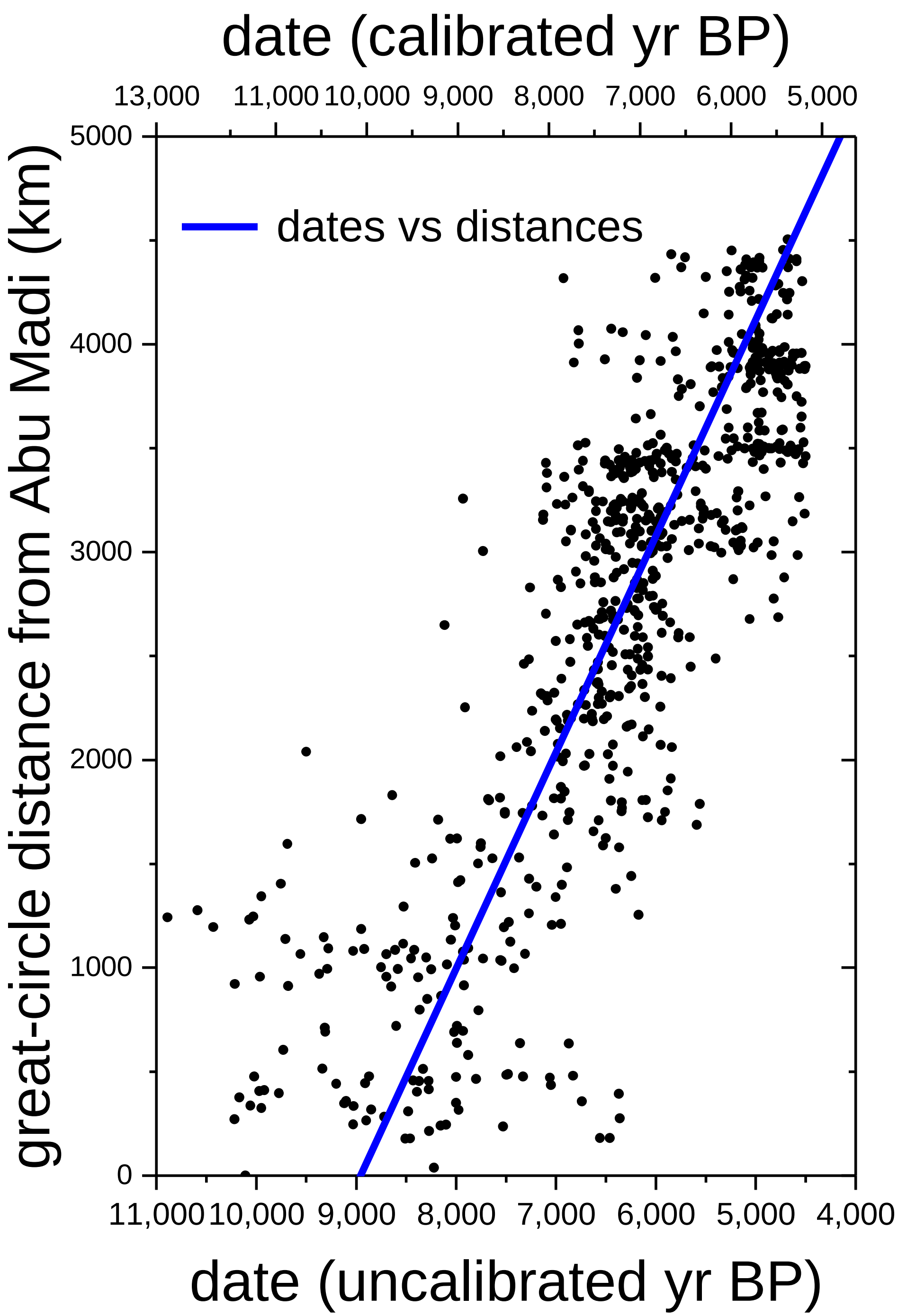
Fort, *PNAS* (2012)

Spread of the Neolihtic in Europe



Fort,
J. R. Soc. Interface
(2015)

What is the observed speed?



What is the observed speed?

0.9-1.3 km/yr

735 sites in Europe & Near East

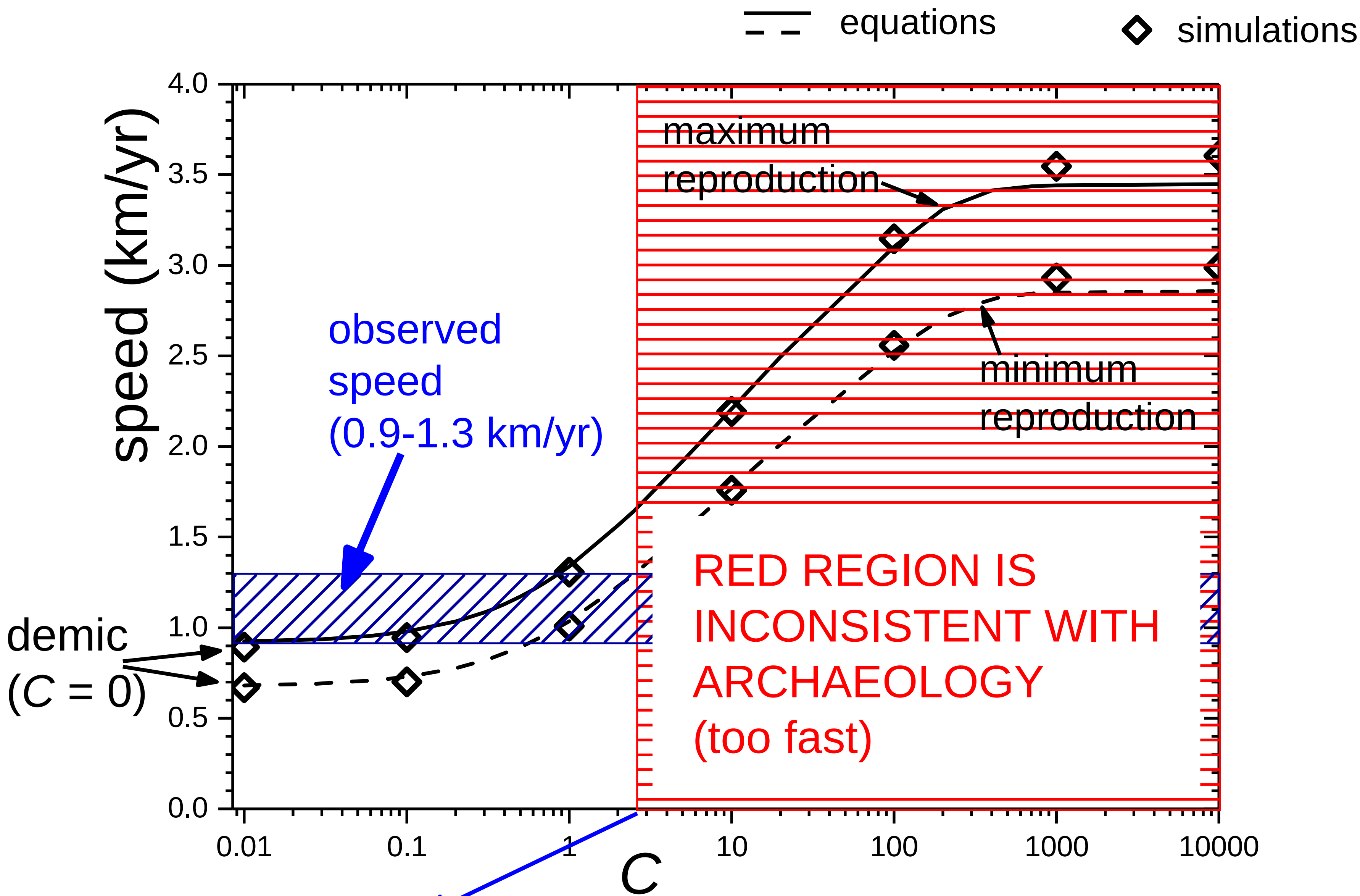
r = 0.83

(highest-*r* origin)

dates vs distances

great circles & shortest paths

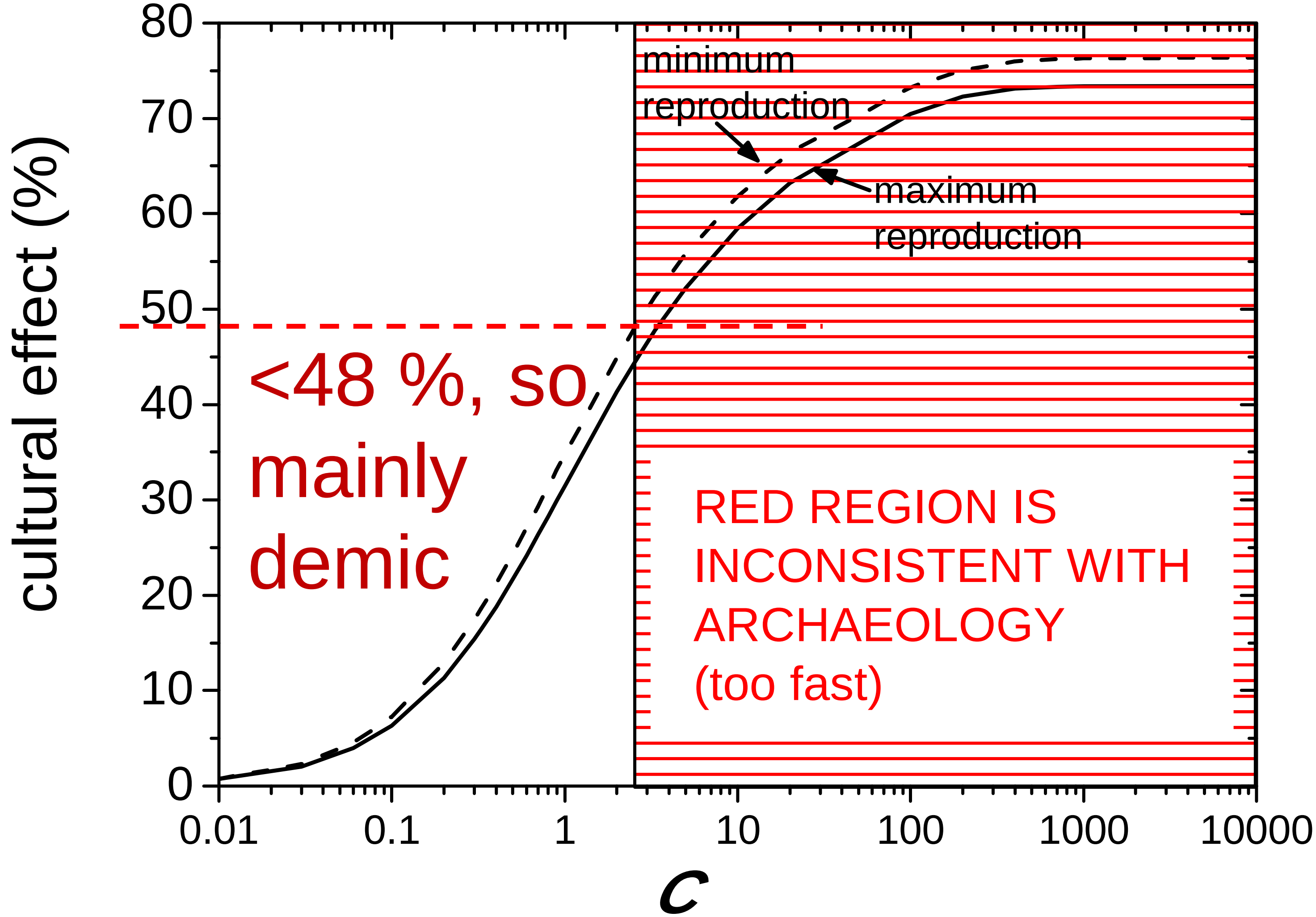
Pinhasi, Fort & Ammerman, *PLoS Biol.* (2005)



$C < 3$, so less than 3 HGs were converted per F per generation

Fort, *PNAS* (2012)

Cultural effect (%) = (speed – demic speed) /speed · 100



Fort, *PNAS* (2012)

Simulations on a grid

They are useful to:

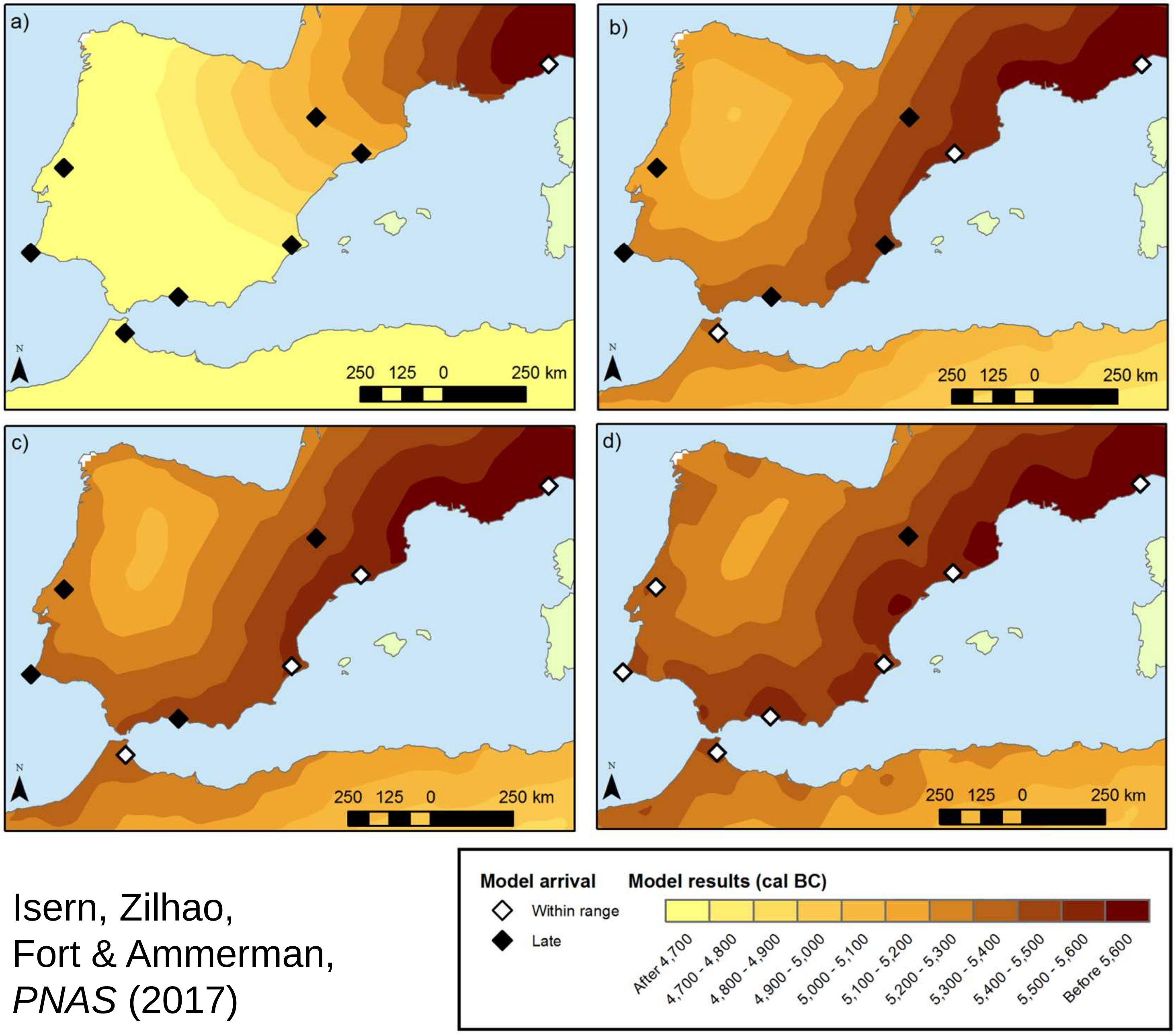
1. check the analytical speed (pevious slides)
2. consider realistic geographies
3. compute genetic clines

Steps in simuations

The following cycle is repeated many times (once per generation) on each node of a **grid** with initially HGs everywhere and Fs only in some region:

1. logistic reproduction (of both populations)
2. cultural transmission (horizontal/oblique or vertical)
3. dispersal (kernel of probability vs distance)

The order of steps does not change the front speed



a) inland travel only

b)-d) also coast travel up to 350 km

b) nearer distances more probable

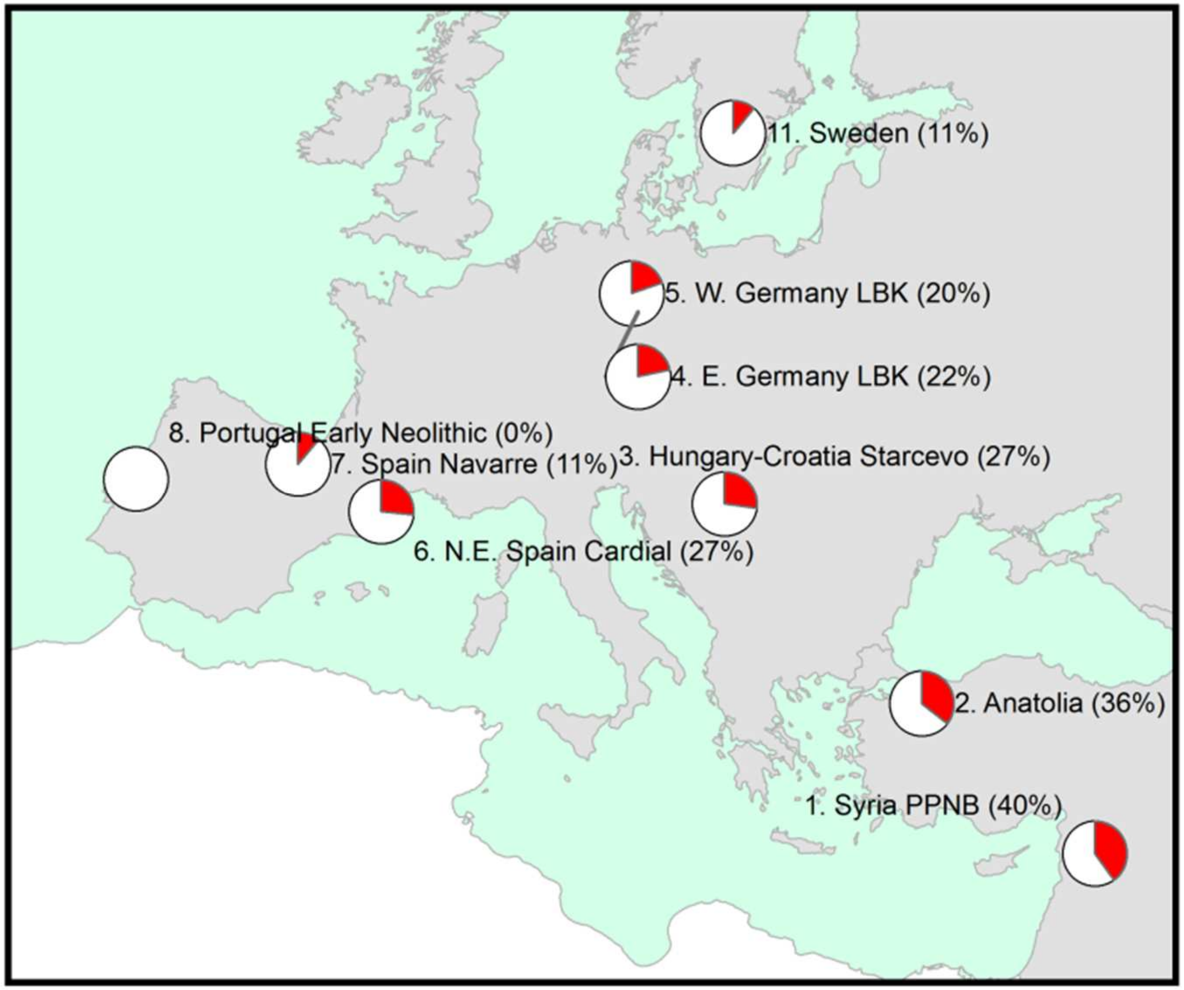
c) all distances equally probable

d) all coast travels of 350 km

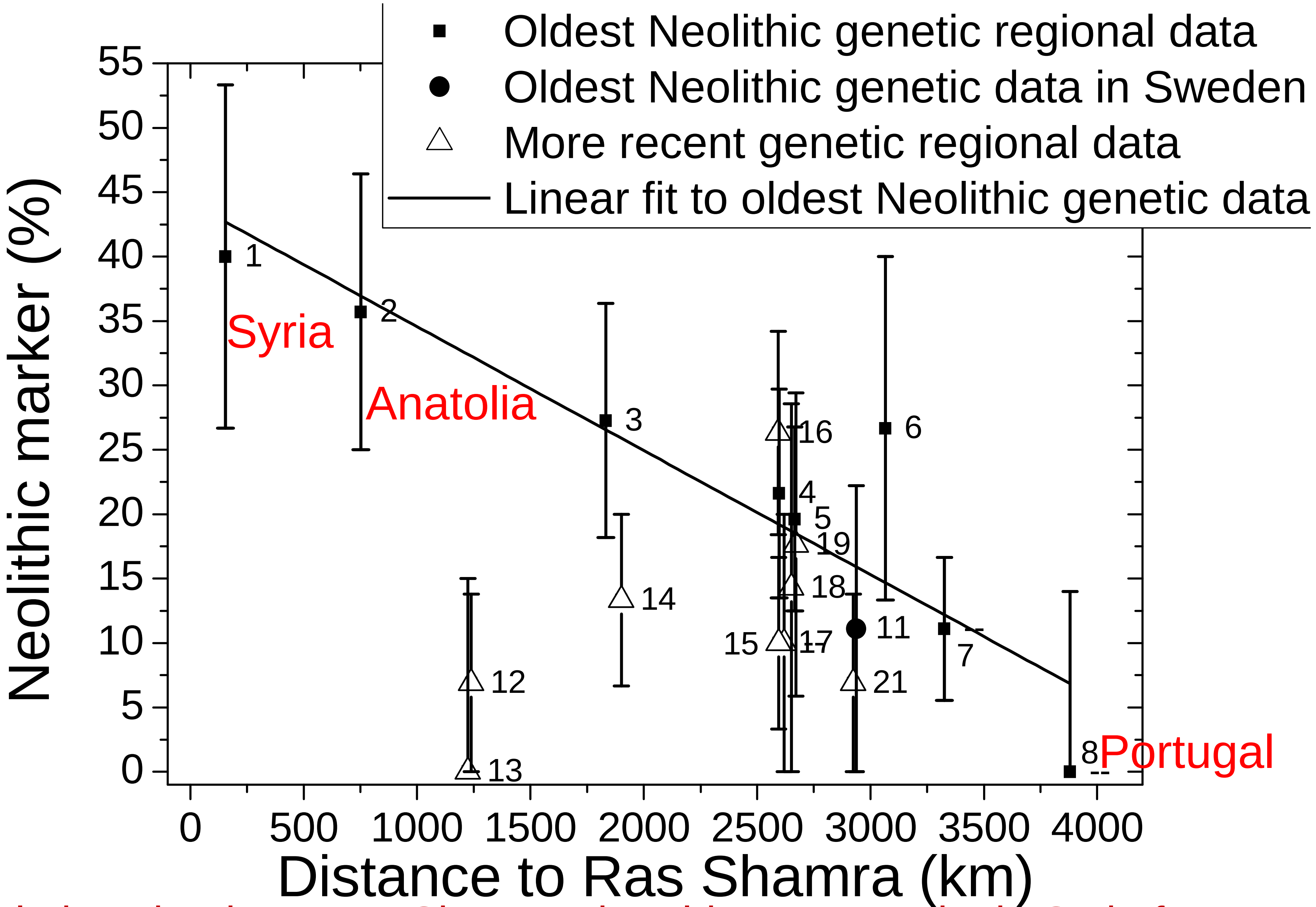
Isern, Zilhao, Fort & Ammerman, *PNAS* (2017)

Ancient genetics

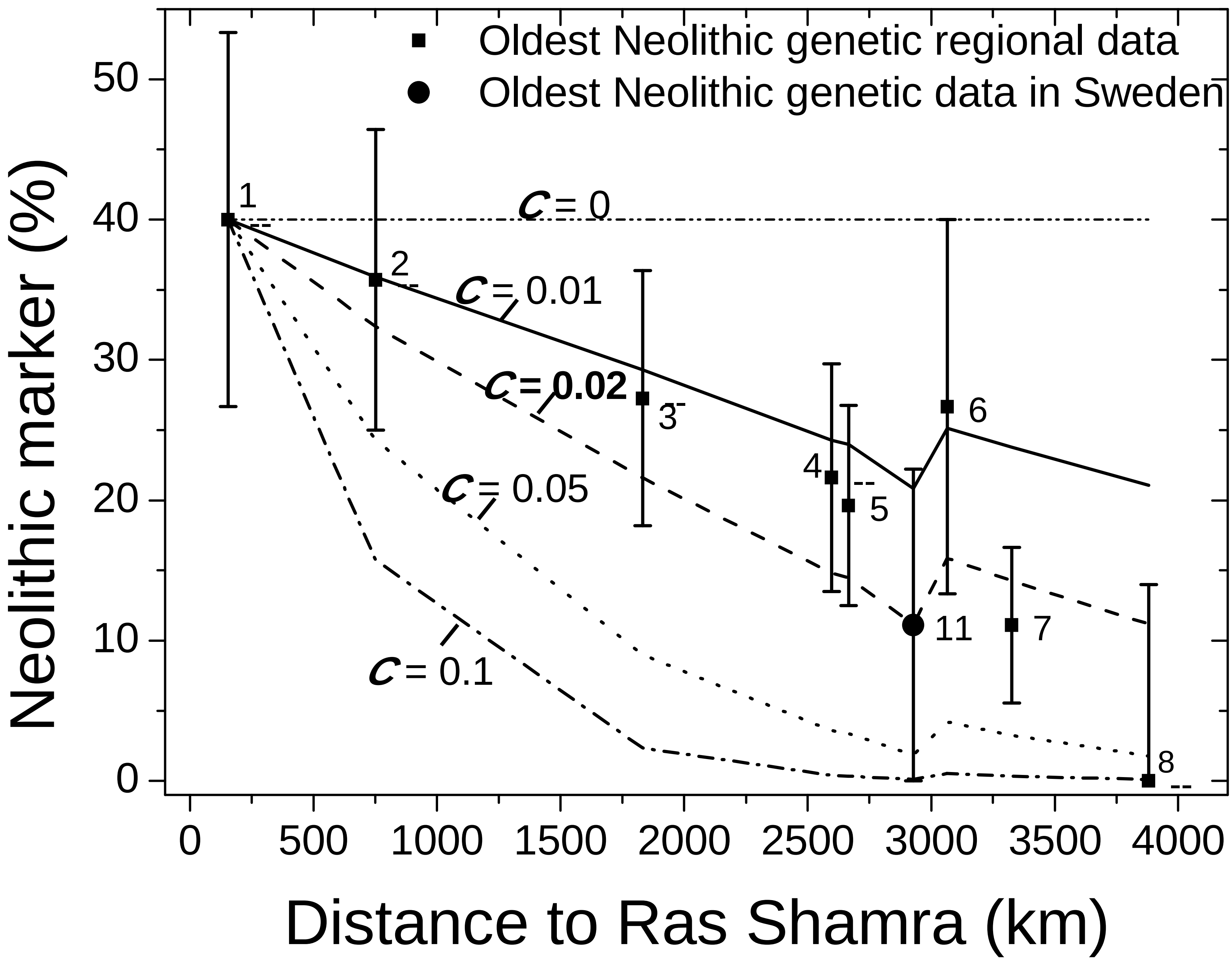
We have gathered a database of all Neolithic individuals (514) whose mtDNA has been determined



We analyze haplogroup K because its frequency (red) decreases Westwards and Nothwards

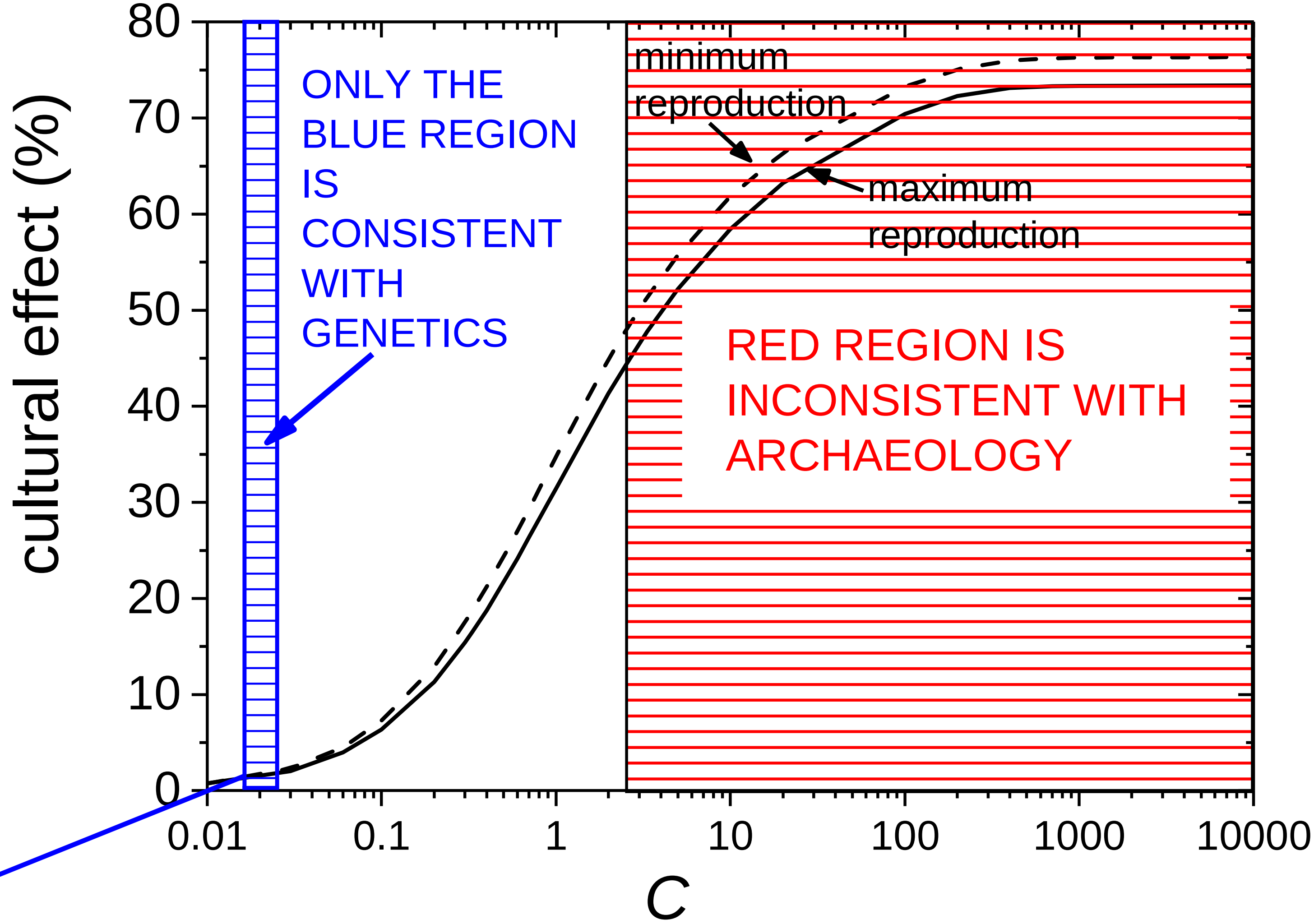


Simulations begin at Ras Shamra, the oldest PPNB site in Syria from Pinhasi, Fort & Ammerman, *PLoS Biol* (2005), at its reported date and with the observed % of haplogroup K in Syria.



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

Effect (%) = (speed – demic speed) /speed · 100



cultural effect of only 2%, so demic>>cultural

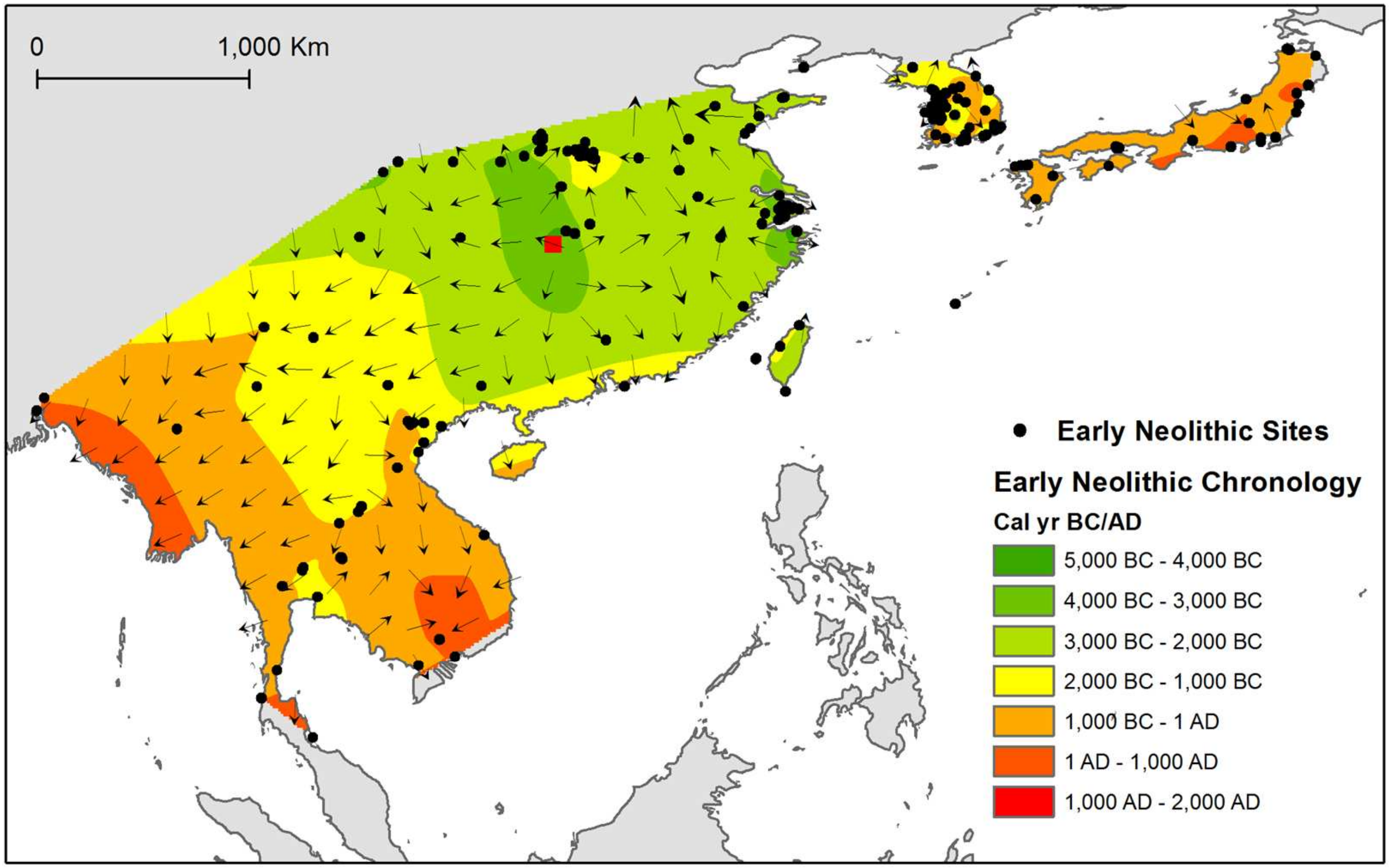
Conclusions on Europe

- **Archaeology:** cultural effect $<48\% \rightarrow$ mainly demic
  and
  $C < 3 \rightarrow < 3$ HGs were converted by every farmer.

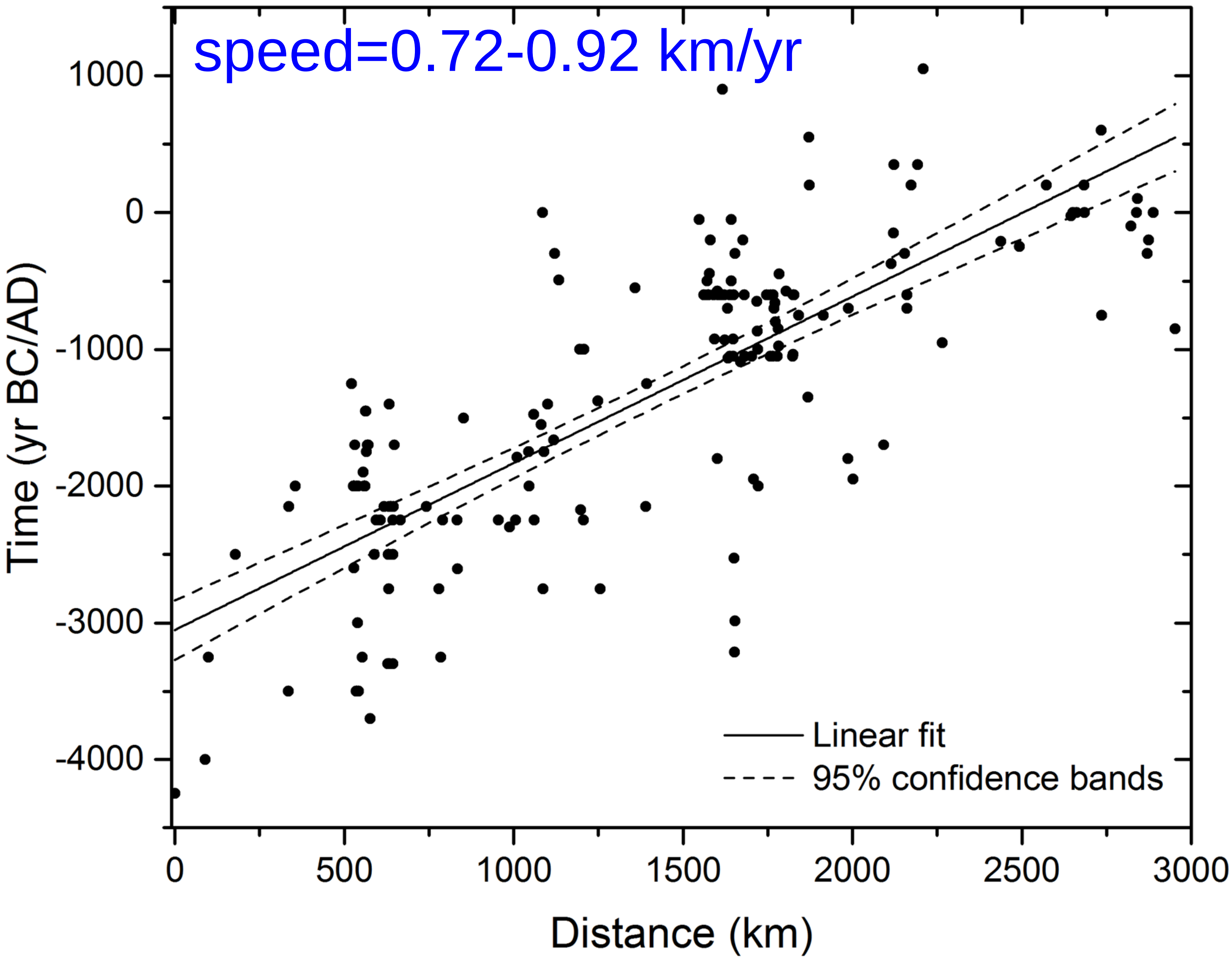
- **Genetics:** cultural effect $\sim 2\% \rightarrow$ demic>>cultural
  and
  $C \approx 0.02 \rightarrow$ only 2 HGs were converted by every 100 Fs; or 2% of Fs interbred with HGs.

Only $\sim 2\%$ of farmers took part in cultural diffusion

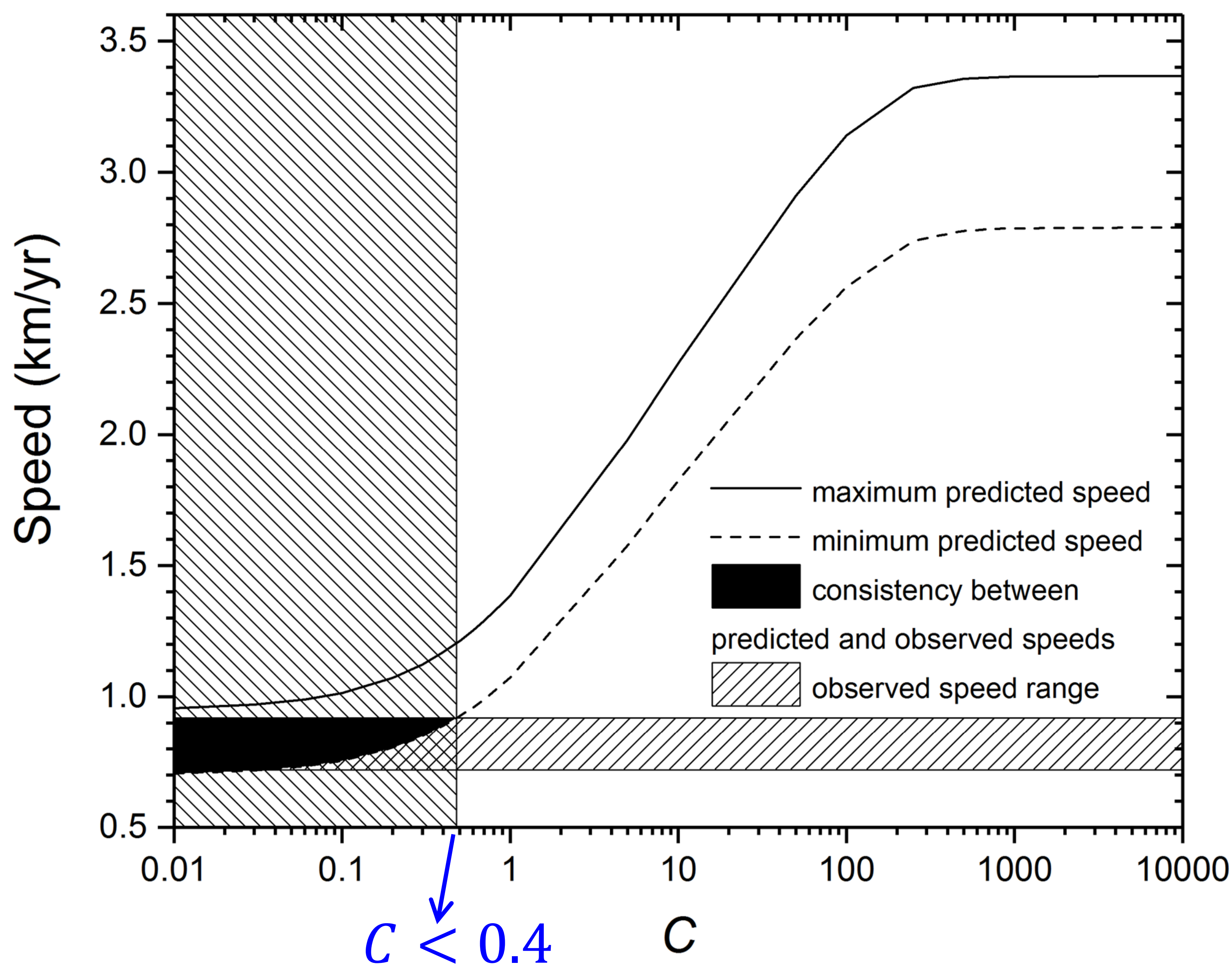
Spread of domesticated rice



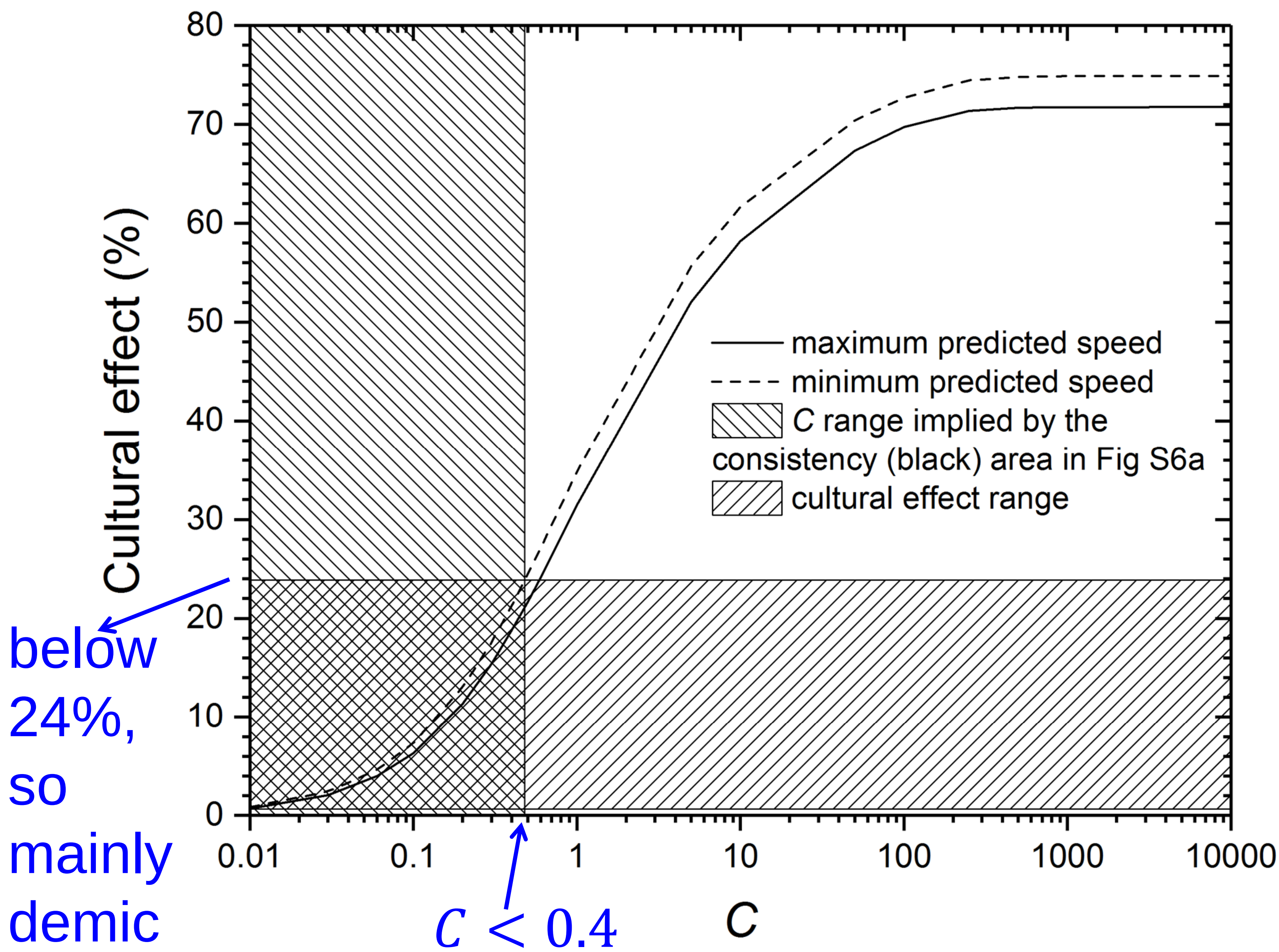
Data from Silva et al., *PLoS One* (2015)
[updated databse of Fuller et al, *The Holocene* (2011)]



Cobo, Fort & Isern, *submitted* (2017)



Speed (km/yr)
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.01
0.1
1
10
100
1000
10000
C
maximum predicted speed
minimum predicted speed
consistency between
predicted and observed speeds
observed speed range
$C < 0.4$



Cultural effect (%)
0
10
20
30
40
50
60
70
80
0.01
0.1
1
10
100
1000
10000
C
maximum predicted speed
minimum predicted speed
C range implied by the consistency (black) area in Fig S6a
cultural effect range
below 24%, so mainly demic
$C < 0.4$

Neolithic case studies

1. Europe: speed ~1 km/yr → mainly <u>demic</u> [1].
2. Domesticated rice in eastern and southeastern Asia:
   speed ~1 km/yr → mainly <u>demic</u> [2].
3. Southwest Asia from Near East:
   speed ~1 km/yr → mainly <u>demic</u> [3].
4. Africa (Bantu): ~1 km/yr → mainly <u>demic</u> [4].

5. Southern Africa (Khoikhoi): >2 km/yr → mainly <u>cultural</u>. The final state was herding, without farming.

[1] Fort, *PNAS* (2012)
[2] Cobo, Fort & Isern, *submitted* (2017)
[3] Comas, Fort, Lancelotti, Ruiz & Madella, *submitted* (2017)
[4] Isern & Fort, *in preparation* (2017)
[5] Jerardino, Fort, Isern & Rondelli, *PLoS One* 2014

Neolithic transitions (this talk)

F= farmers

H=hunter-gatherers

Front speeds (from archaeological data) give maximum values for the % of cultural diffusion and the % of farmers involved in cultural transmission (teaching and/or interbreeding).

Genetic clines give more precise values.

'Cultural History of PaleoAsia' project

F= modern humans

H=Neanderthals

Front speeds (from archaeological data) could give maximum values for the % of cultural diffusion and the % of modern humans involved in cultural transmission (teaching and/or interbreeding).

Genetic clines could give more precise values.

Questions?