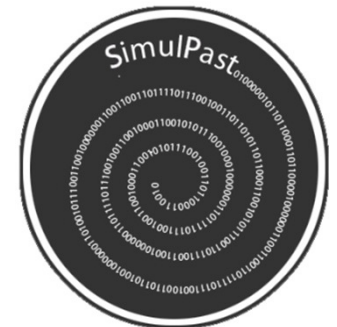


The Neolithic transition: diffusion of people or diffusion of culture?

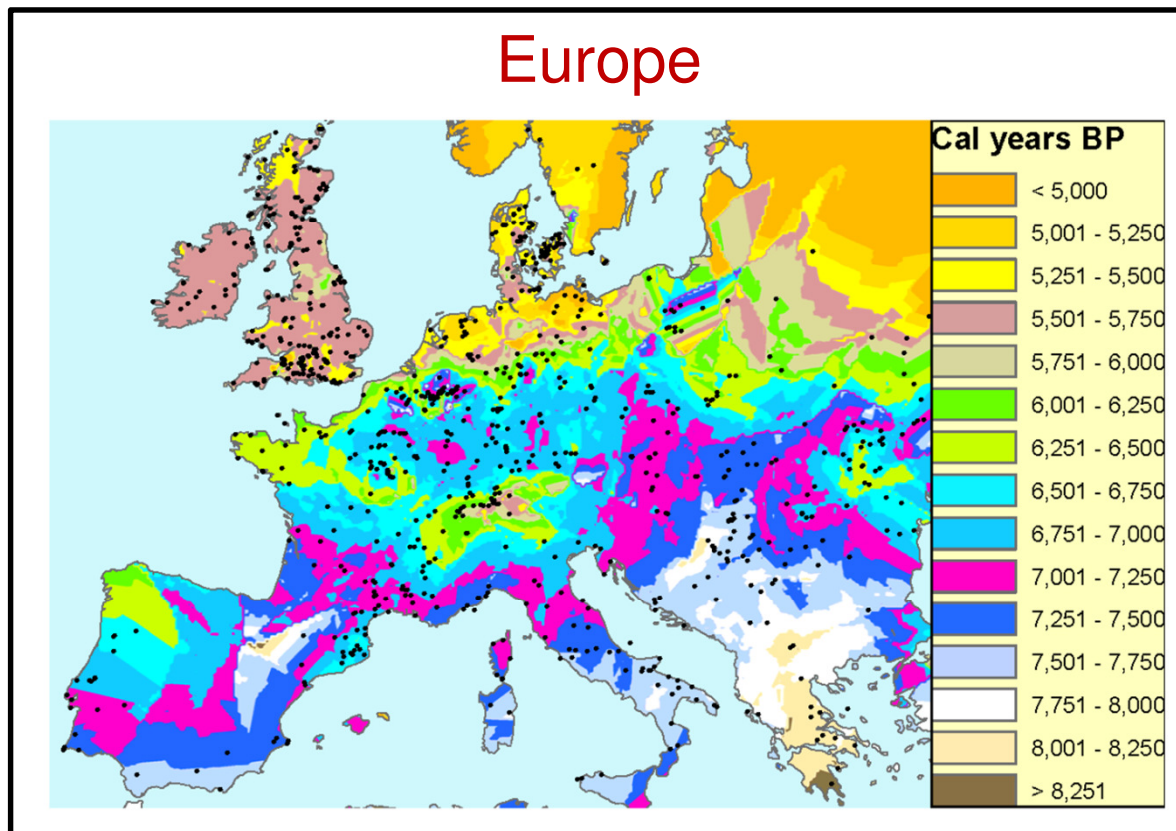
Joaquim Fort
Universitat de Girona (Catalonia, Spain)



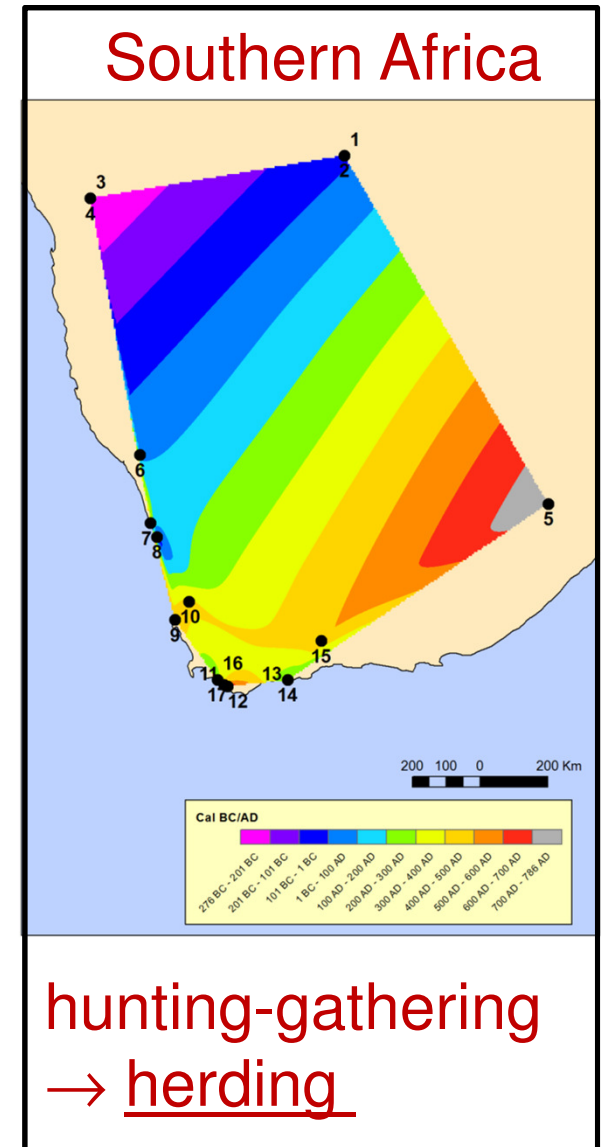
Diffusion Fundamentals VI
Dresden
August 24th, 2015



Neolithic transition =
hunting-gathering →
farming or herding



hunting-gathering → farming
and stockbreeding



hunting-gathering
→ herding

Models of Neolithic transitions

- Demic diffusion = spread of farming populations = dispersal + net reproduction
- Cultural diffusion = spread of ideas = transmission of plants, animals and knowledge from farmers to hunter-gatherers (acculturation).
- Demic-cultural models

Acculturation

Cavalli-Sforza & Feldman (*book* 1979)
Boyd & Richerson (*book* 1985)
Fort (*PNAS* 2012)

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

$$\left\{ \begin{array}{l} \text{farmers (F): } P'_F = P_F + f \frac{P_F P_H}{P_F + \gamma P_H} \\ \text{hunter - gatherers (H): } P'_H = P_H - f \frac{P_F P_H}{P_F + \gamma P_H} \end{array} \right.$$

f = intensity of cultural transmission

γ = preference of H s to copy F s rather than H s (if $\gamma < 1$)

Lotka-Volterra equations

$$P'_F = P_F + \eta P_F P_H \quad (1)$$

$$P'_H = P_H - \eta P_F P_H \quad (2)$$

They have 2 problems:

1) They are not derived from cultural transmission theory

2) Number of HGs converted per farmer

according to Eq. (1): $\frac{P'_F - P_F}{P_F} = \eta P_H \rightarrow \infty!$ No maximum!
if $P_H \rightarrow \infty$

Cavalli-Sforza & Feldman (book 1979)
Fort (PNAS 2012)

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

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

if $P_H \gg P_F$:

$\frac{P'_F - P_F}{P_F} = C$ is the number of H s converted by farmer
 $\frac{P'_F - P_F}{P_F}$ is not ∞ , in contrast to Lotka-Volterra eqs.

The front speed does not depend on f and γ separately, but only on the number of HGs converted by farmer, $C = \frac{f}{\gamma}$.

Demic-cultural models

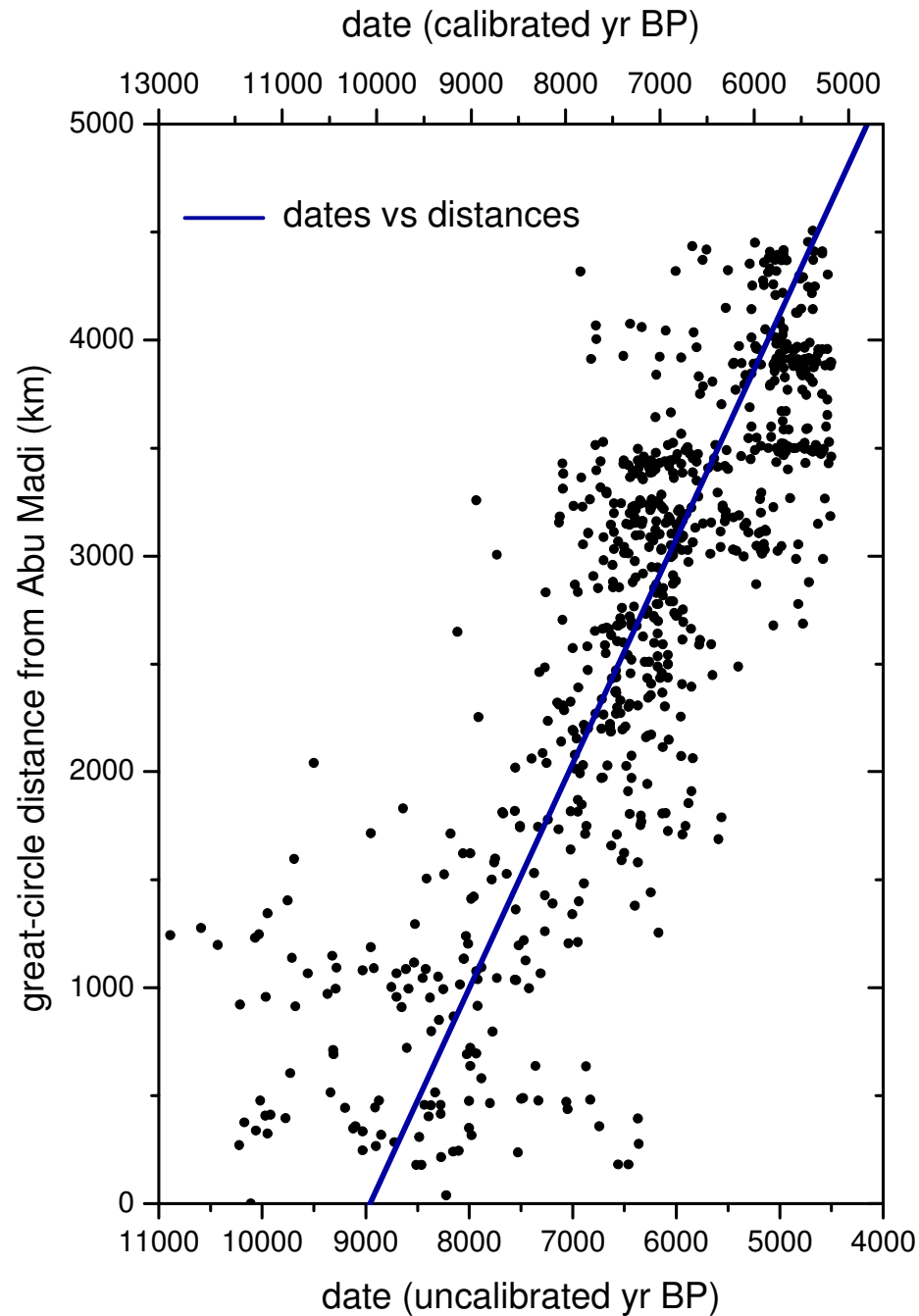
Fort (*PNAS* 2012)

Steps:

1. reproduction (logistic)
2. cultural transmission (acculturation)
3. dispersal (distance kernel)

The order of steps does not change the speed

This cycle is repeated many times (once per generation)



Up to now we have discussed models.

What is the observed speed?

0.9-1.3 km/yr

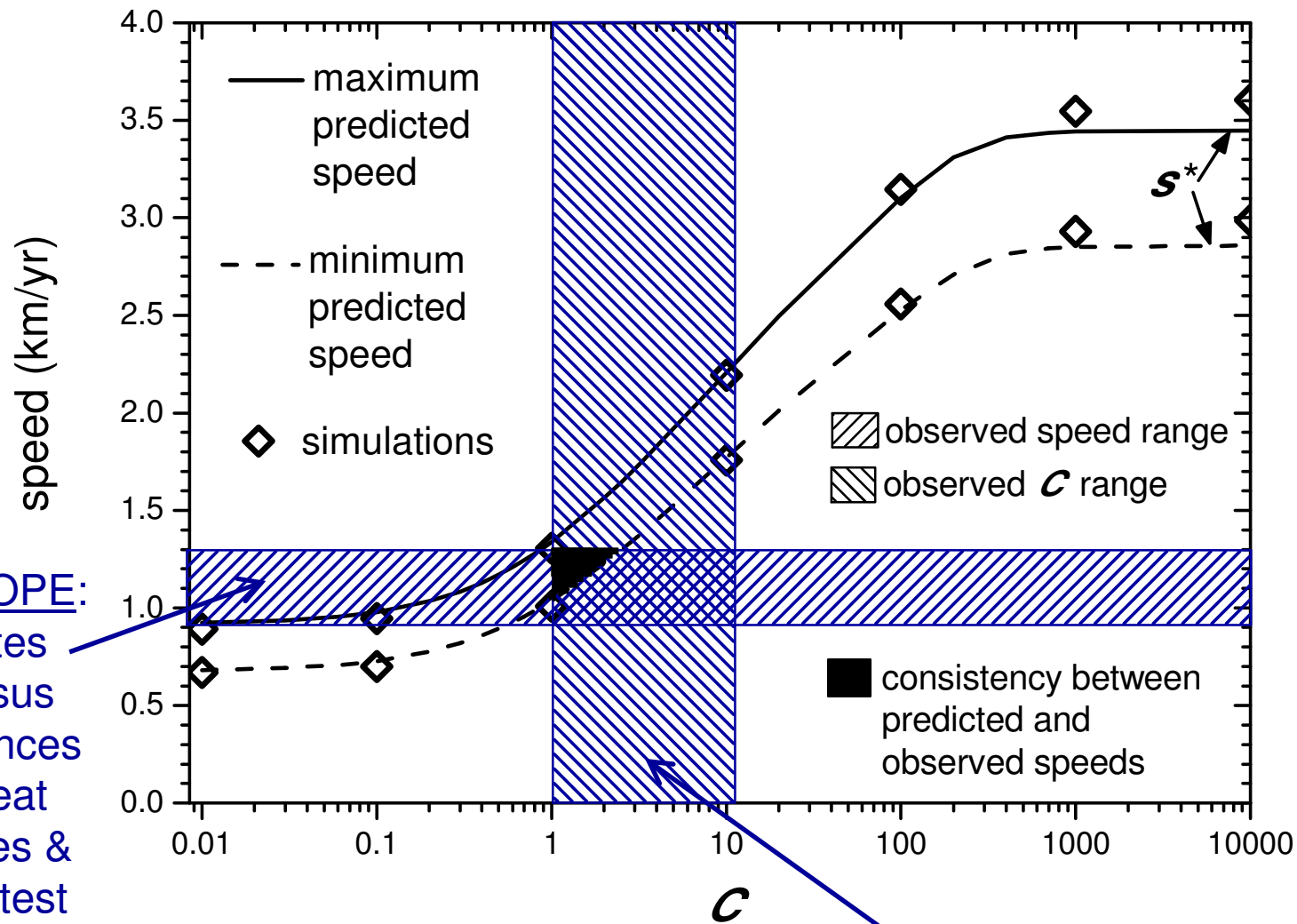
735 sites in Europe & Near East

$r = 0.83$ (highest- r origins, great circles & shortest paths)

Pinhasi, Fort & Ammerman,

PLoS Biol. (2005)

Effect of acculturation intensity C on the front speed in Europe



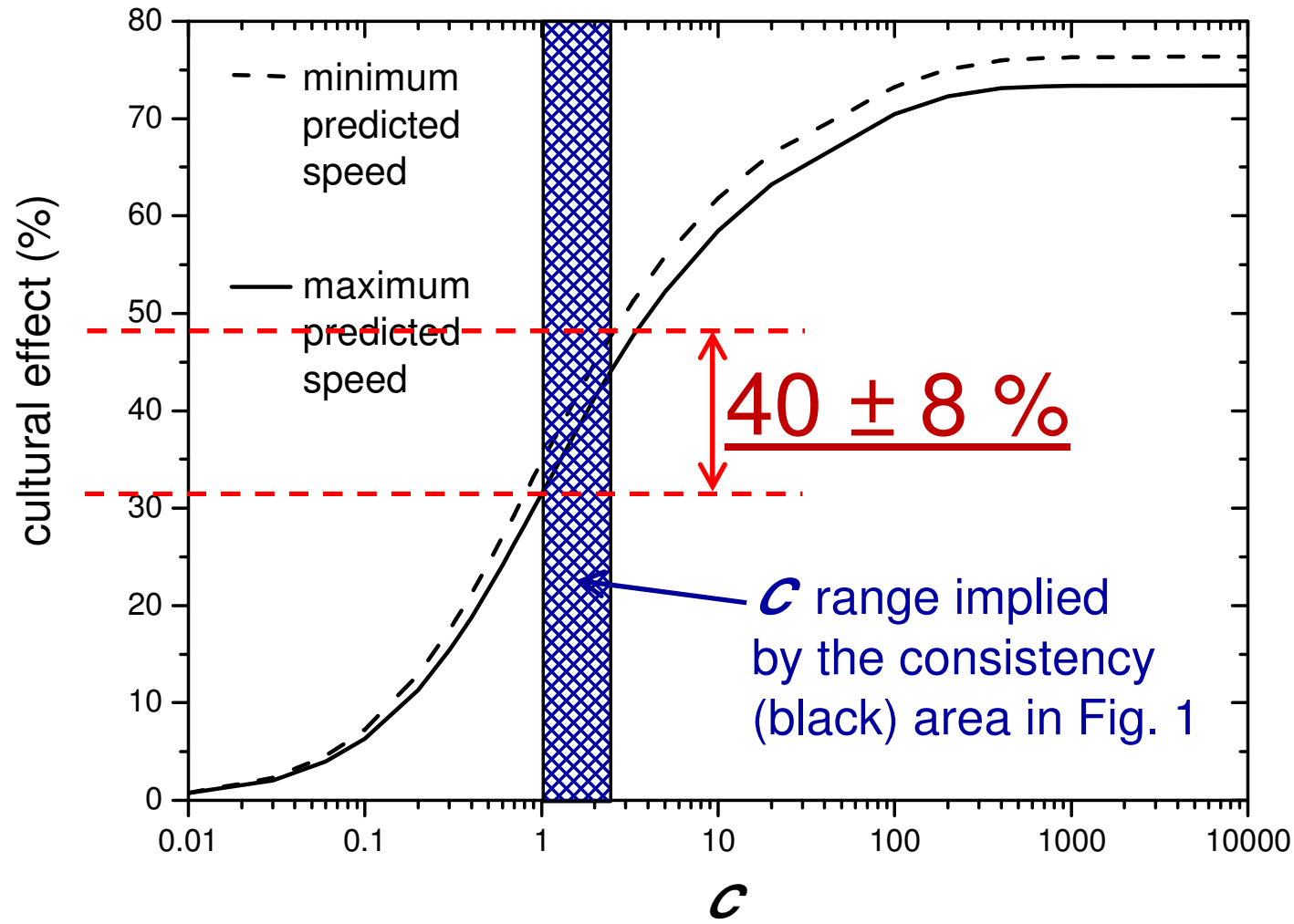
EUROPE:
Dates
versus
distances
(great
circles &
shortest
paths)

Ache hunter-gatherers (Paraguay)

Fort,
PNAS
(2012)

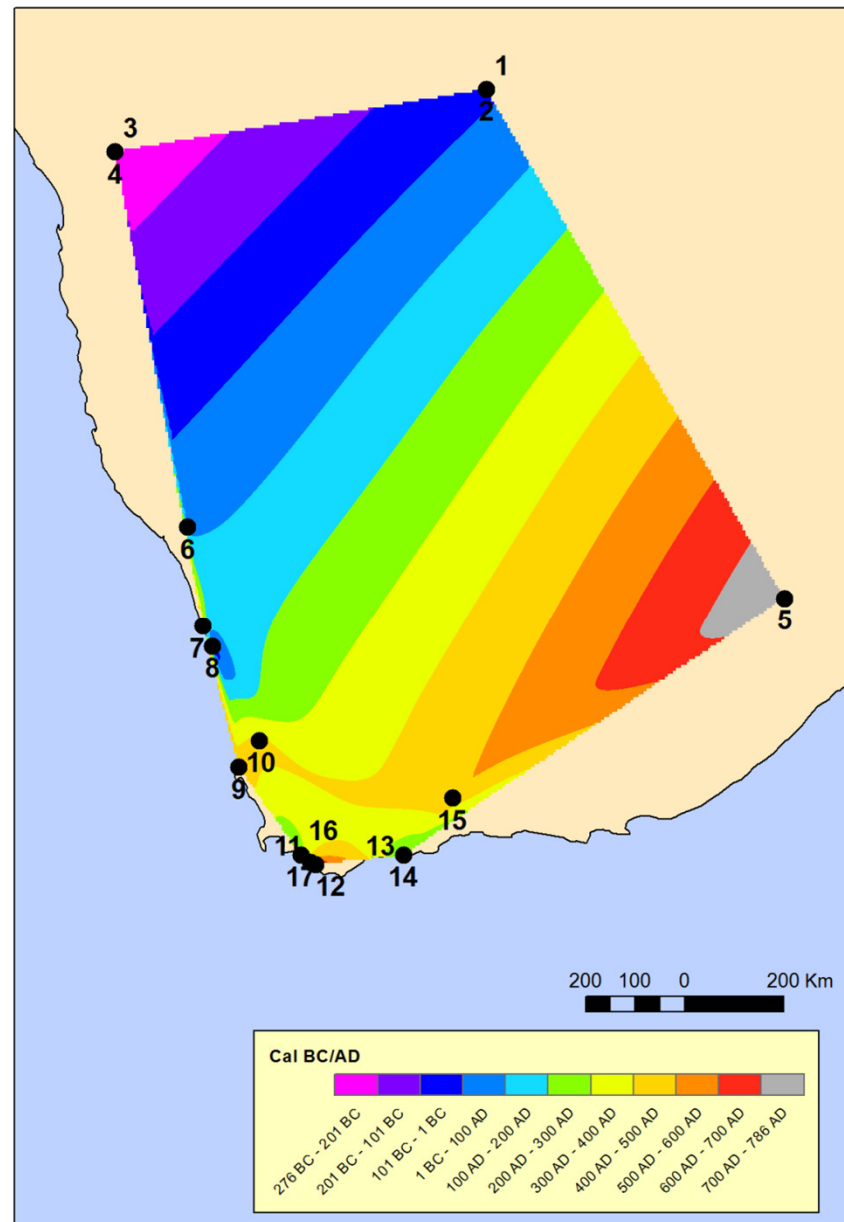
Effect of cultural diffusion in Europe

$$\text{Effect (\%)} = (\text{speed} - \text{demic speed}) / \text{speed} \cdot 100$$



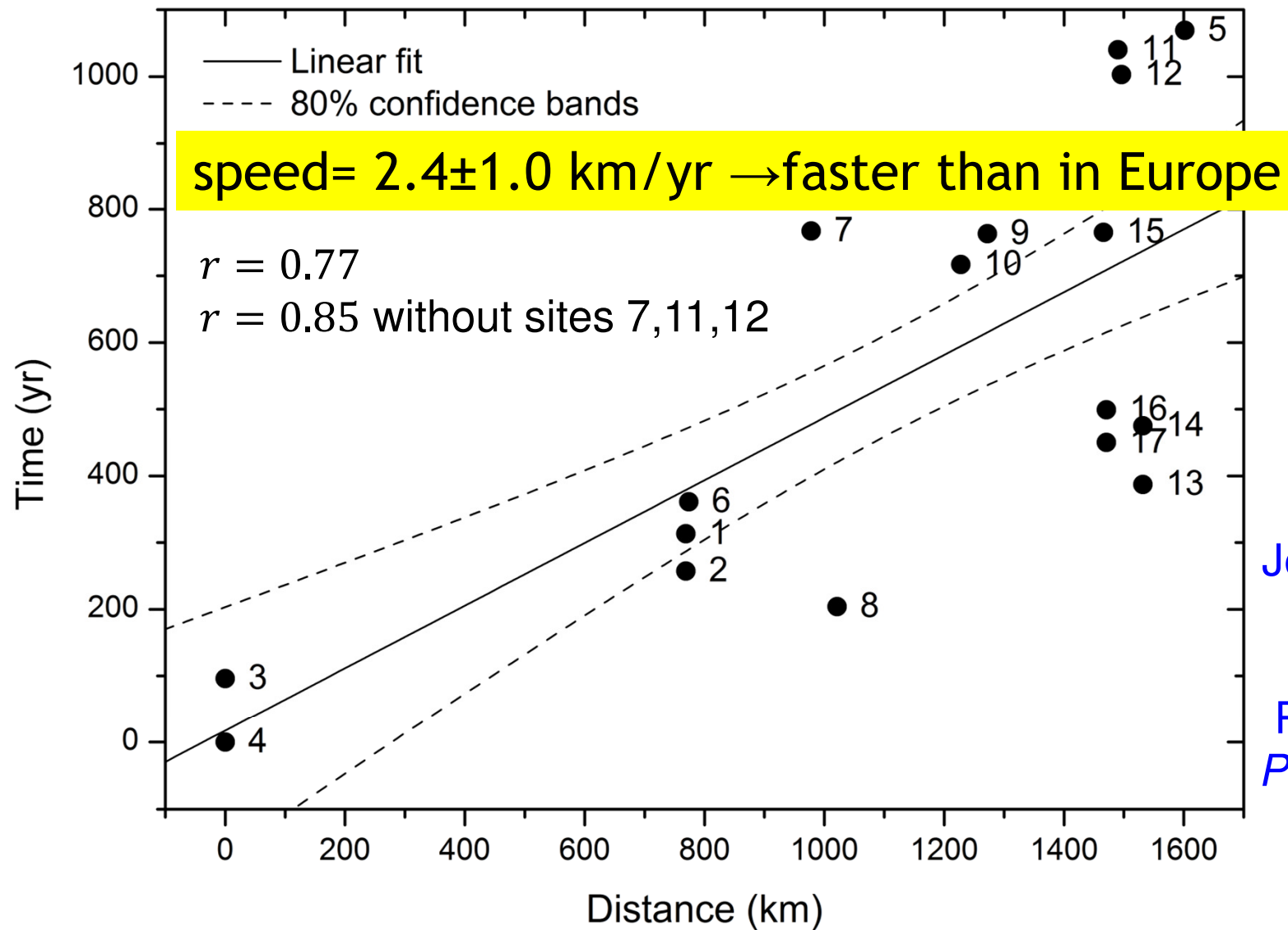
Fort,
PNAS
(2012)

The Neolithic transition in southern Africa



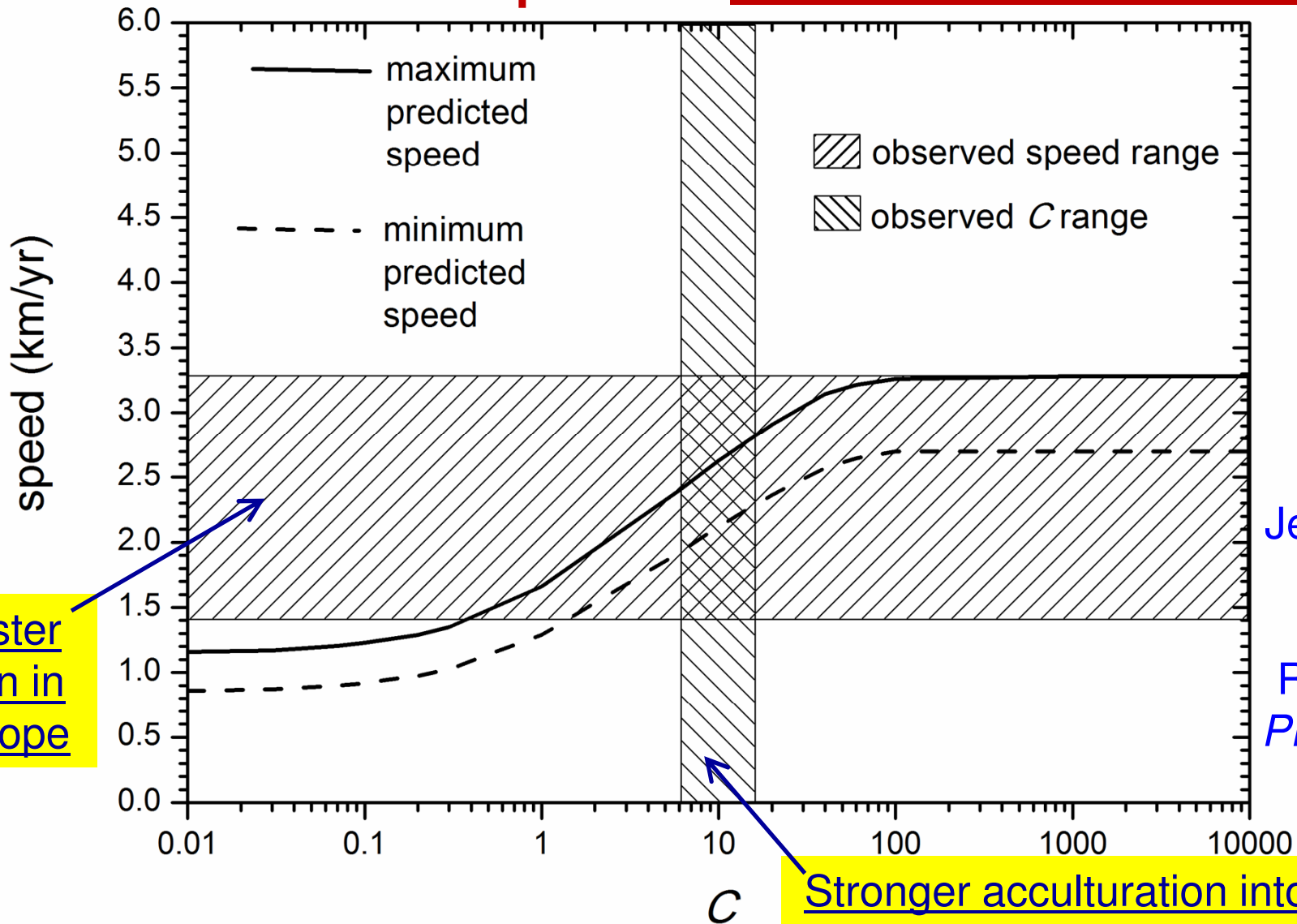
Jerardino,
Fort,
Isern,
Rondelli,
PLoS One
(2014)

The Neolithic transition in southern Africa



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

Effect of acculturation intensity C on the front speed in southern Africa



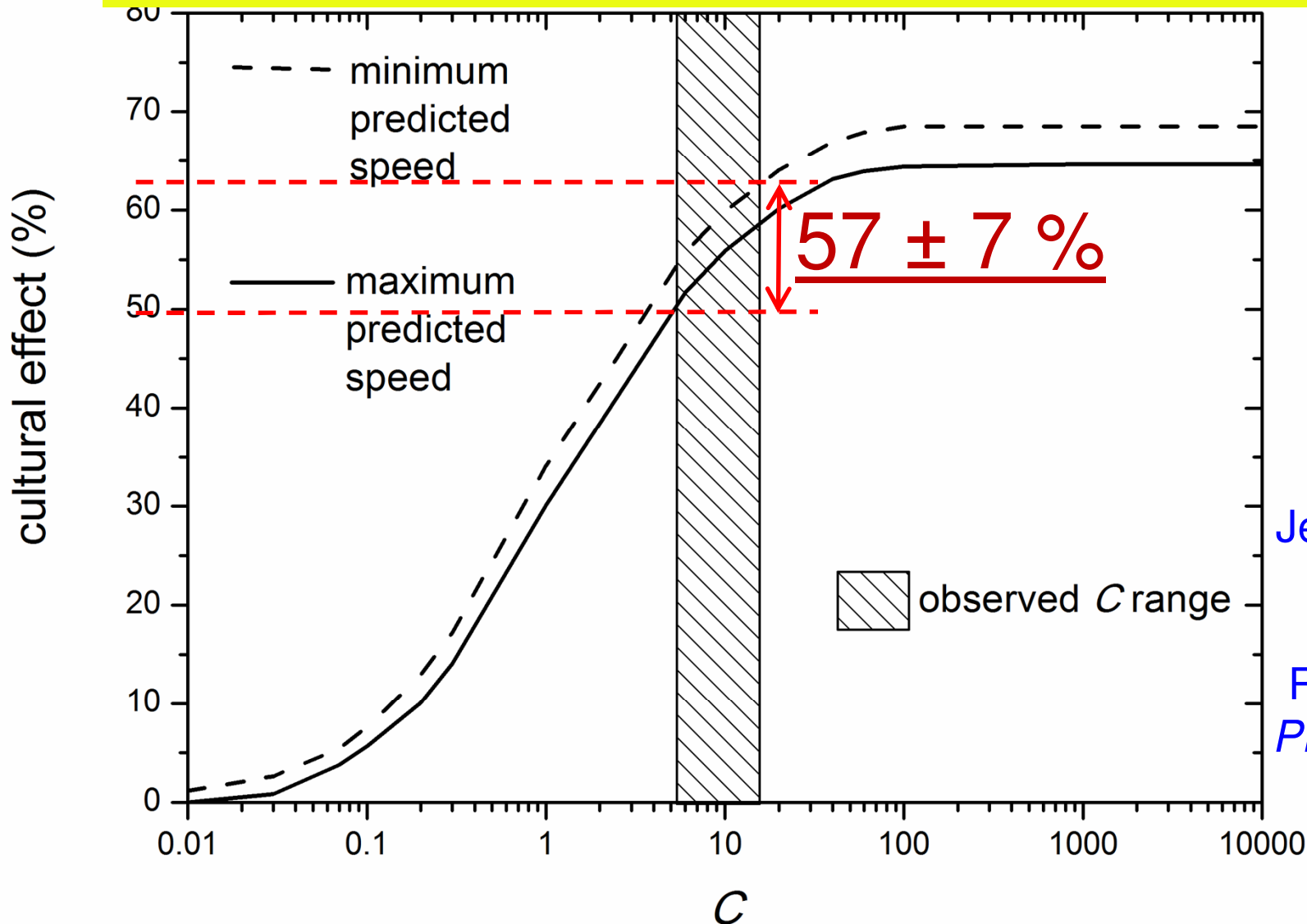
Faster than in Europe

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

Stronger acculturation into herding than into farming

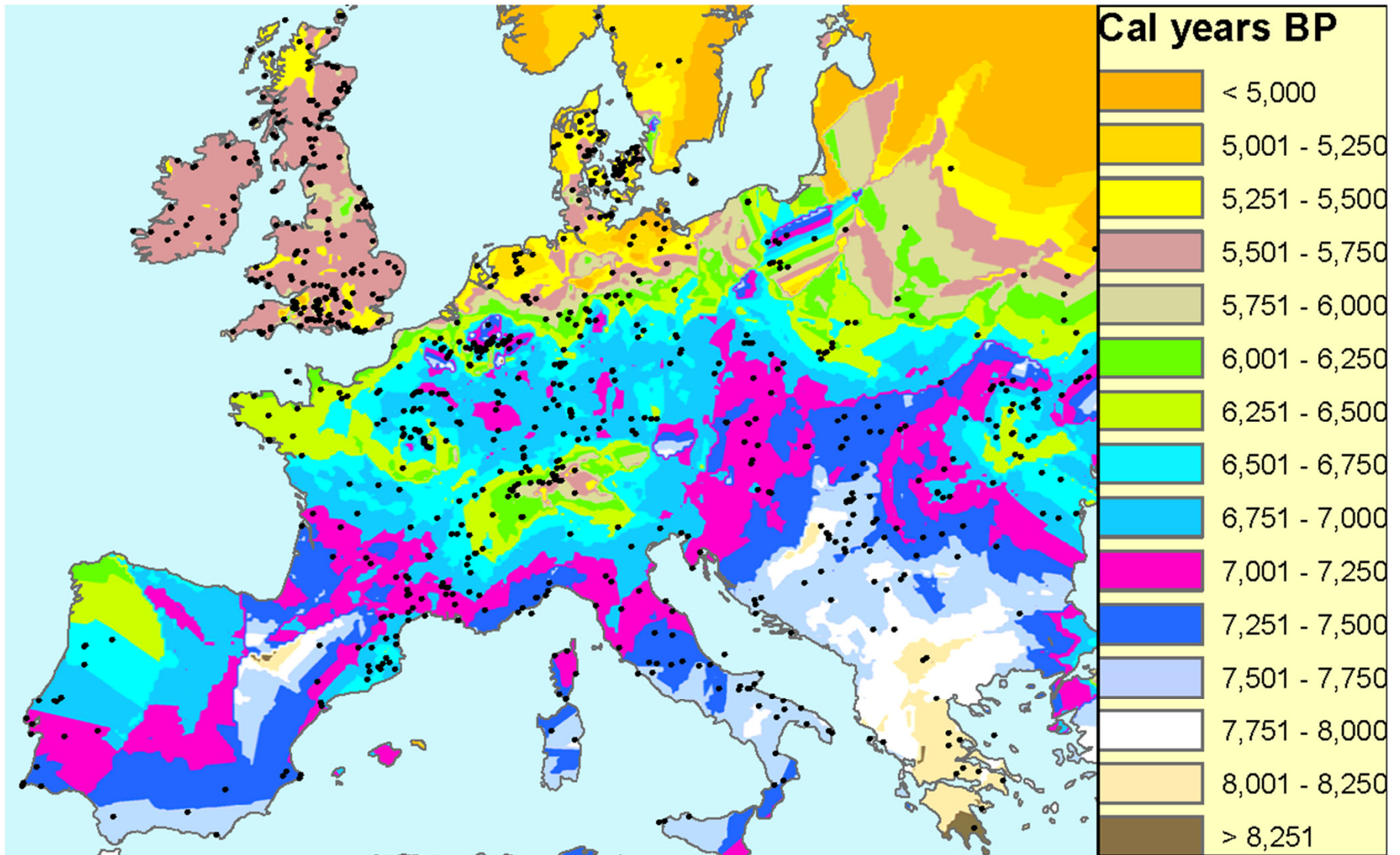
Effect of cultural diffusion in southern Africa

$$\text{Effect (\%)} = (\text{speed} - \text{demic speed}) / \text{speed} \cdot 100$$

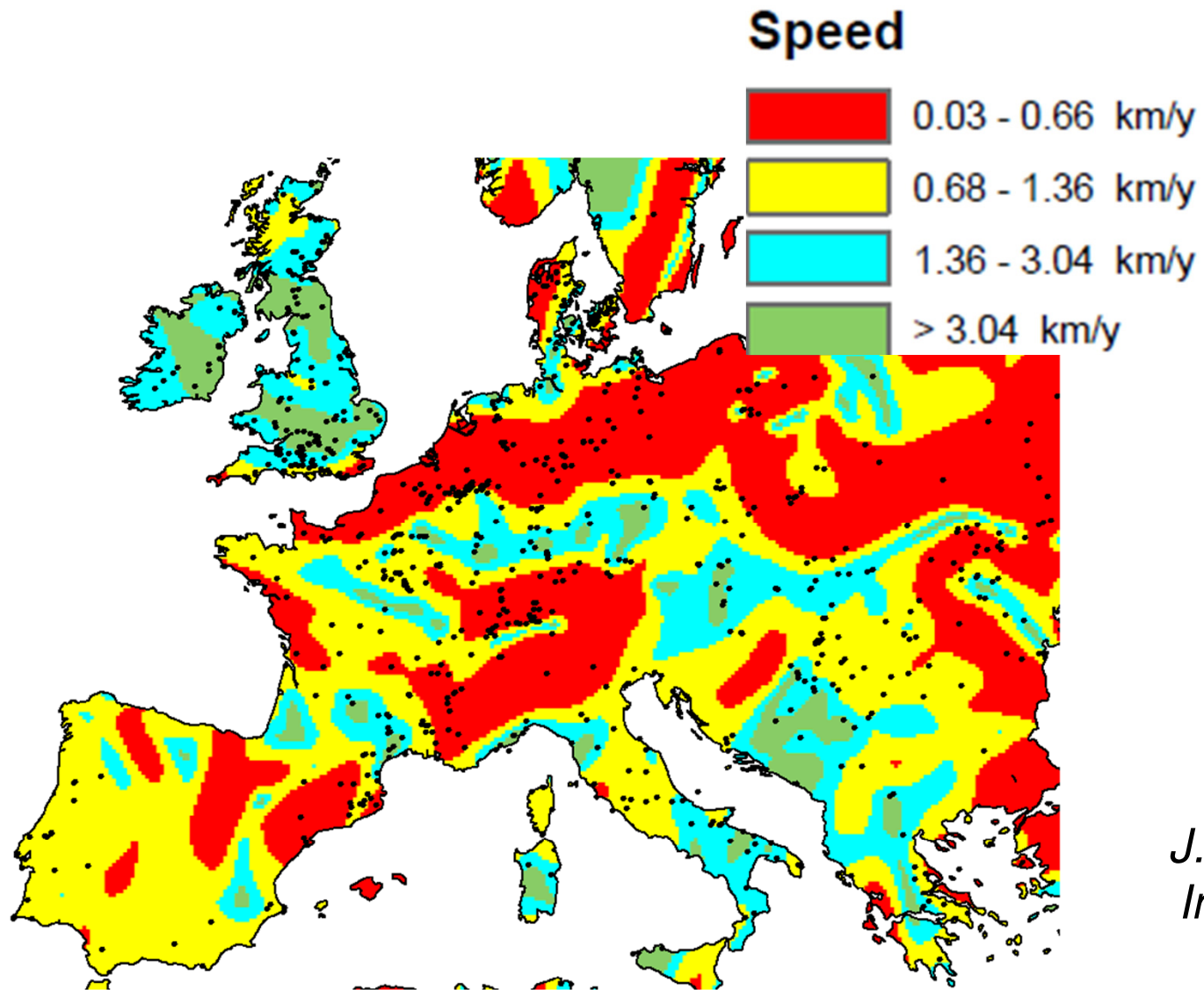


Jerardino,
Fort,
Isern,
Rondelli,
PLoS One
(2014)

Local features in Europe



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



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

The previous maps show observed speeds.

What are the speeds from the models?

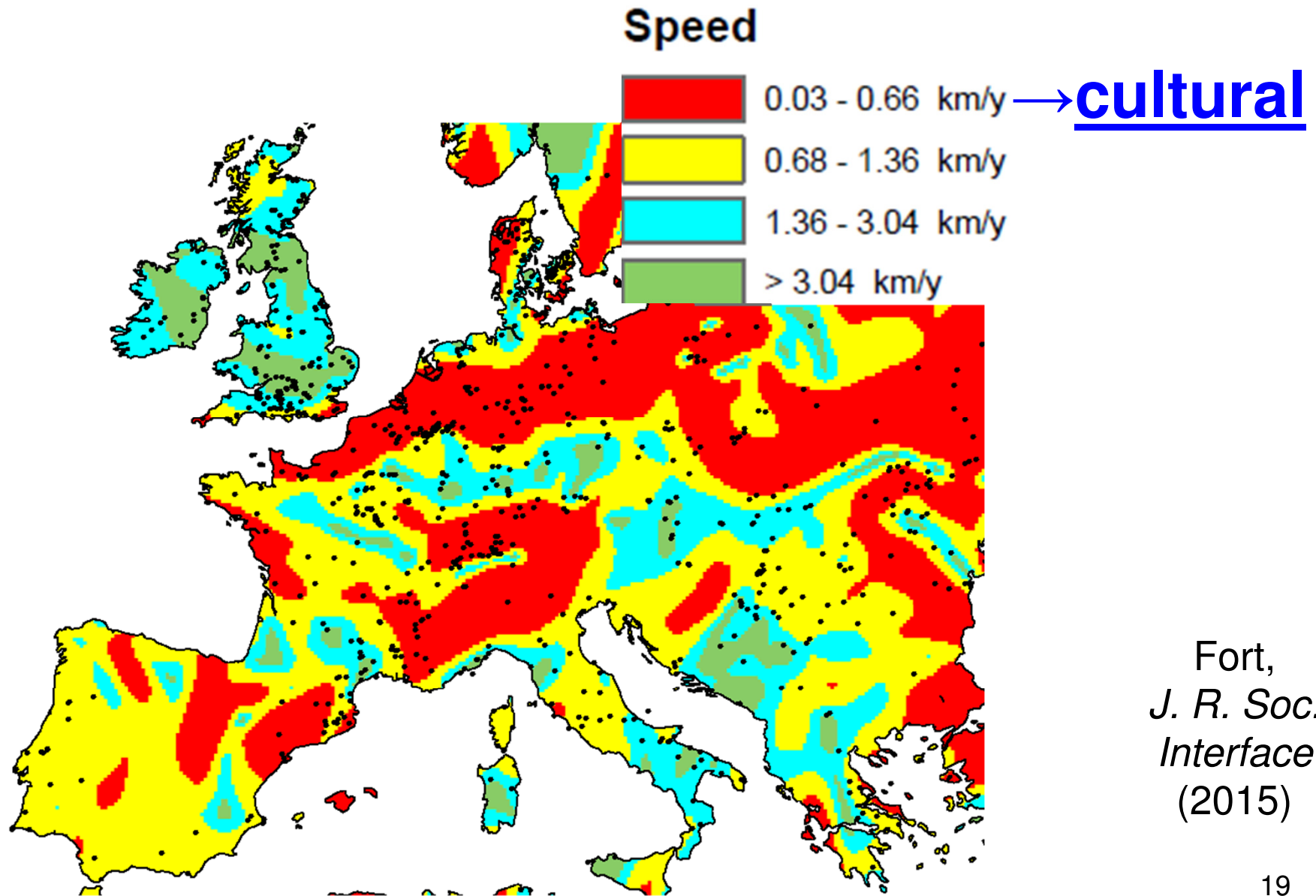
1. Purely cultural model
2. Purely demic model
3. Demic-cultural model

Purely cultural model

- Population 1 (Mbuti, band I): $\{P_k\}=\{0.59, 0.37, 0.04\}$,
 $\{R_k\}=\{2.5, 7.5, 12.5\}$ km \rightarrow **0.17-0.36 km/y.**
- Population 2 (Mbuti, band II): $\{P_k\}=\{0.12, 0.30, 0.43, 0.15\}$,
 $\{R_k\}=\{2.5, 7.5, 12.5, 17.5\}$ km \rightarrow **0.30-0.57 km/y.**
- Population 3 (Mbuti, band III): $\{P_k\}=\{0.20, 0.41, 0.26, 0.08, 0.05\}$,
 $\{R_k\}=\{2.5, 7.5, 12.5, 17.5, 22.5\}$ km \rightarrow **0.32-0.66 km/y. MAX**
- Population 4 (Aka): $\{P_k\}=\{0.12, 0.25, 0.11, 0.04, 0.03, 0.16, 0.05,$
 $0.05, 0.05, 0.14\}$, $\{R_k\}=\{0.05, 0.1, 0.2, 0.25, 0.3, 0.4, 2,3,5,6\}$ km
 \rightarrow **0.09-0.19 km/y.**
- Population 5 (Baka): $\{P_k\}=\{0.48, 0.04, 0.13, 0.14, 0.18, 0.03\}$,
 $\{R_k\}=\{0, 0.5, 0.8, 1.5, 1.7, 2.7\}$ km \rightarrow **0.03-0.07 km/y. MIN**

Overall range: **0.03-0.66 km/y** (cultural model)

Interpretation of the observed speeds



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

Purely demic model

- Population A (Gilishi 15): $\{p_j\}=\{0.54, 0.17, 0.04, 0.25\}$,
 $\{r_j\}=\{2.4; 14.5, 36.3, 60.4\}$ km \rightarrow **0.87-1.15 km/y.**
- Population B (Gilishi 25): $\{p_j\}=\{0.40, 0.17, 0.17, 0.26\}$,
 $\{r_j\}=\{2.4; 14.5, 36.3, 60.4\}$ km \rightarrow **0.92-1.21 km/y.**
- Population C (Shiri 15): $\{p_j\}=\{0.19, 0.07, 0.22, 0.52\}$,
 $\{r_j\}=\{2.4; 14.5, 36.2, 60.4\}$ km \rightarrow **1.14-1.48 km/y. MAX**
- Population D (Yanomano): $\{p_j\}=\{0.19, 0.54, 0.17, 0.04, 0.04, 0.02\}$,
 $\{r_j\}=\{5, 30, 50, 70, 90, 110\}$ km \rightarrow **1.12-1.48 km/y.**
- Population E (Issongos): $\{p_j\}=\{0.42; 0.23; 0.16; 0.08; 0.07; 0.02; 0.01; 0.01\}$,
 $\{r_j\}=\{2.3, 7.3, 15, 25, 35, 45, 55, 100\}$ km \rightarrow **0.68-0.92 km/y. MIN**

Overall range: **0.68 -1.48 km/y** (purely demic model)

For 0.68 km/y, obviously 0% cultural.

But for 0.7, 0.8, 0.9, ... km/y, what is the cultural %?

s_{obs} = observed speed

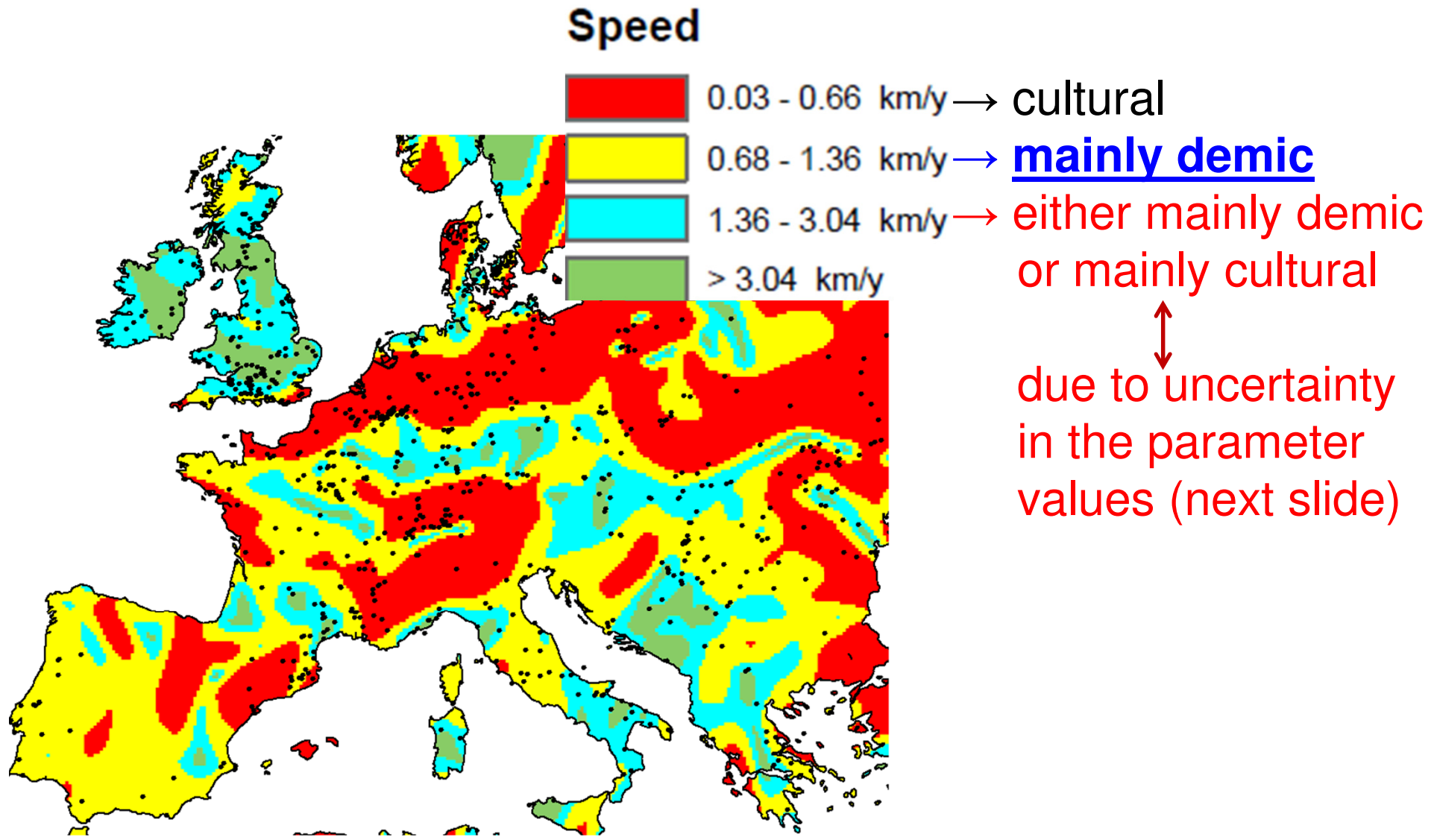
s_D = speed predicted by the purely demic model

$$\text{Cultural effect (in \%)} = E = \frac{s_{obs} - s_D}{s_{obs}} 100$$

$$s_D \text{ min} = 0.68 \text{ km/y} \rightarrow E_{max} = \left(1 - \frac{0.68}{s_{obs}}\right) 100 \rightarrow$$

$E_{max} < 50\%$ if $s_{obs} < 1.36 \text{ km/y}$: mainly demic regions (yellow in the map)

Interpretation of the observed speeds



Effect of parameter uncertainty

Example: Let us see that $s_{obs} = 1.6$ km/y can be either mainly demic or mainly cultural:

$$\text{Cultural effect (in \%)} = E = \frac{s_{obs} - s_D}{s_{obs}} 100$$

- Demic kernel C $\rightarrow s_D = 1.4$ km/y \rightarrow

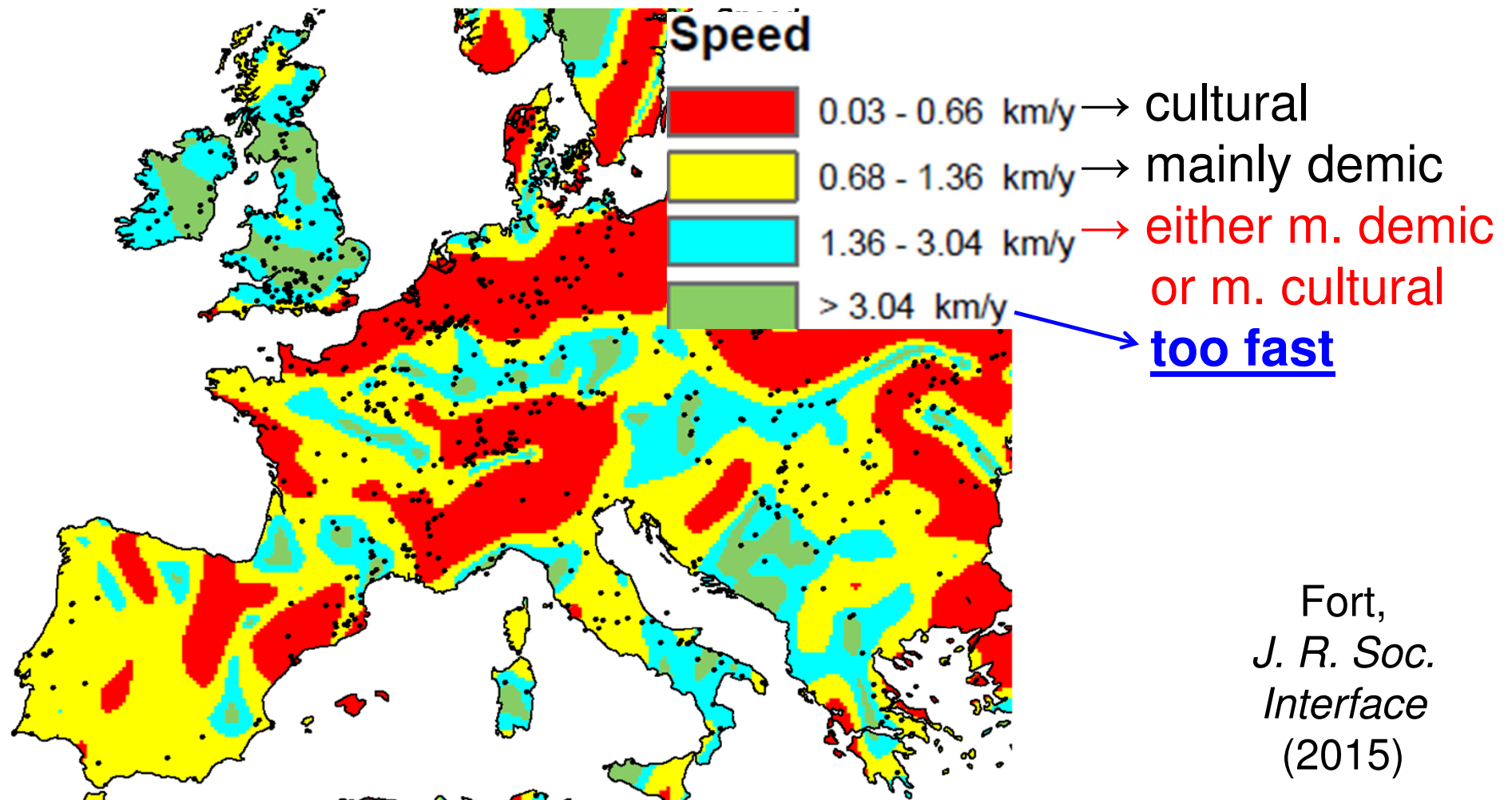
$$E = \frac{1.6 - 1.4}{1.6} 100 = 13\% < 50\% \text{ mainly demic}$$

- Demic kernel E $\rightarrow s_D = 0.7$ km/y \rightarrow

$$E = \frac{1.6 - 0.7}{1.6} 100 = 56\% > 50\% \text{ mainly cultural !}$$

This leads to regions with either mainly demic or mainly cultural diffusion (blue color in the map)

Interpretation of the observed speeds



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

Fig. 3

Interpretation of the observed speeds

- **Mainly demic diffusion** (yellow) was fast (speeds above 0.68 km/y). Areas: **Greece, Italy, the Balkans, Hungary, Slovakia, Czechia and central Germany.**

This includes a substantial part of the Linearbandkeramic (LBK) culture in Central Europe*. It agrees with Bogucki (2003) and Shennan & Edinborough (2007).

- **Cultural diffusion** (red) was slow (speeds below 0.66 km/y). Areas: **Northern Europe, the Alps and West of the Black Sea** (red color). This agrees, respectively, with Bogucki (1996), Clark (1990) and Anthony (2007).

*Kaczanowska M, Kozłowski JK, 2003, Fig. 12.7

Open problem

These results use parameter values which are not fitted but estimated from independent data. But are the parameter values used realistic?

It would help a lot to measure prehistoric dispersal kernels, if possible:

- Strontium isotope: not accurate distances
- Genetics: identification of parent-child pairs?

Until we have accurate parameter values, the models can be useful but the conclusions are preliminary.

Appendix

Mathematical models

Fort, JRS Interface (2015), Supp. Info.

In the pre-school yesterday, you derived Fisher's model:

$$\frac{\partial N}{\partial t} = D_N \nabla^2 N + a_N N \left(1 - \frac{N}{K_N}\right) \rightarrow v = 2\sqrt{a_N D_N}$$

N = population density of the Neolithic population

This is a demic model.

This model causes an error of 30% !

It is more precise to use a cohabitation model (next slide).

Cohabitation models

1) Purely demic model

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

$$\text{Logistic reproduction: } R_T [N(x, y, t)] = \frac{e^{a_N T} K_N N(x, y, t)}{K_N + (e^{a_N T} - 1) N(x, y, t)}$$

$\phi_N(\Delta_x, \Delta_y)$ is a set of probabilities p_j for farmers to disperse at distances r_j during a generation time T .

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

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

Cohabitation models

2) Demic-cultural model

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

$$\int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \phi_N(\Delta_x, \Delta_y) d\Delta_x d\Delta_y \int_{-\infty}^{\infty} \int_{-\infty}^{\infty} \phi'_P(\Delta'_x, \Delta'_y) d\Delta'_x d\Delta'_y$$

$$R_T \left[f \frac{N(x + \Delta_x + \Delta'_x, y + \Delta_y + \Delta'_y, t) P(x + \Delta_x, y + \Delta_y, t)}{N(x + \Delta_x + \Delta'_x, y + \Delta_y + \Delta'_y, t) + \gamma P(x + \Delta_x, y + \Delta_y, t)} \right]$$

$\phi'_P(\Delta'_x, \Delta'_y)$ is a set of probabilities P_k for hunter-gatherers to learn agriculture from farmers living at distances R_k during a generation time T .

$$v = \min_{\lambda > 0} \frac{a_N T + \ln\left[\left(\sum_{j=1}^M p_j I_0(\lambda r_j)\right)\left(1 + C \left[\sum_{k=1}^Q P_k I_0(\lambda R_k)\right]\right)\right]}{T\lambda}$$

with $C = f/\gamma$

- If $C=0 \rightarrow$ purely demic model (shown 2 slides before)
- If $p_j=1$ for $r_j=0$ km \rightarrow purely cultural model