Neolithic transitions: demic diffusion, cultural diffusion and cultural evolution

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Keynote speaker

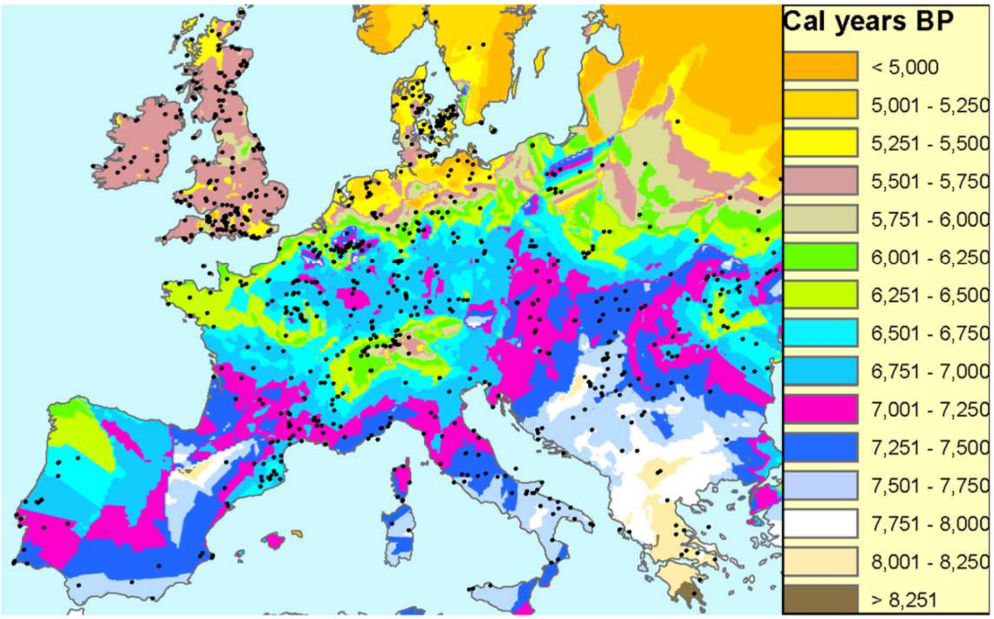
The connected past meeting

Imperial College London

September 9th, 2014

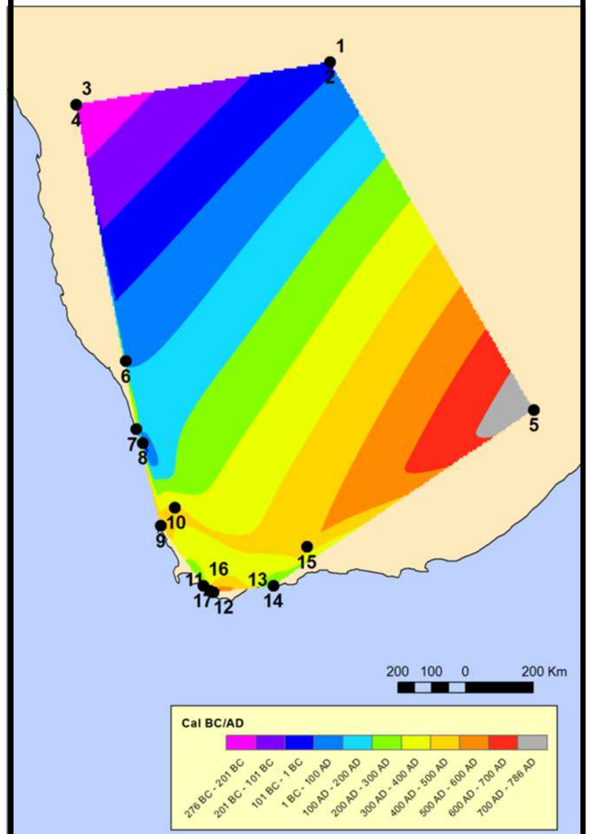
Neolithic transitions

Europe



hunting-gathering →<u>farming</u>
and stockbreeding

Southern Africa



hunting-gathering
→ <u>herding</u>

The Neolithic transition is the shift from hunting-gathering into farming or herding.

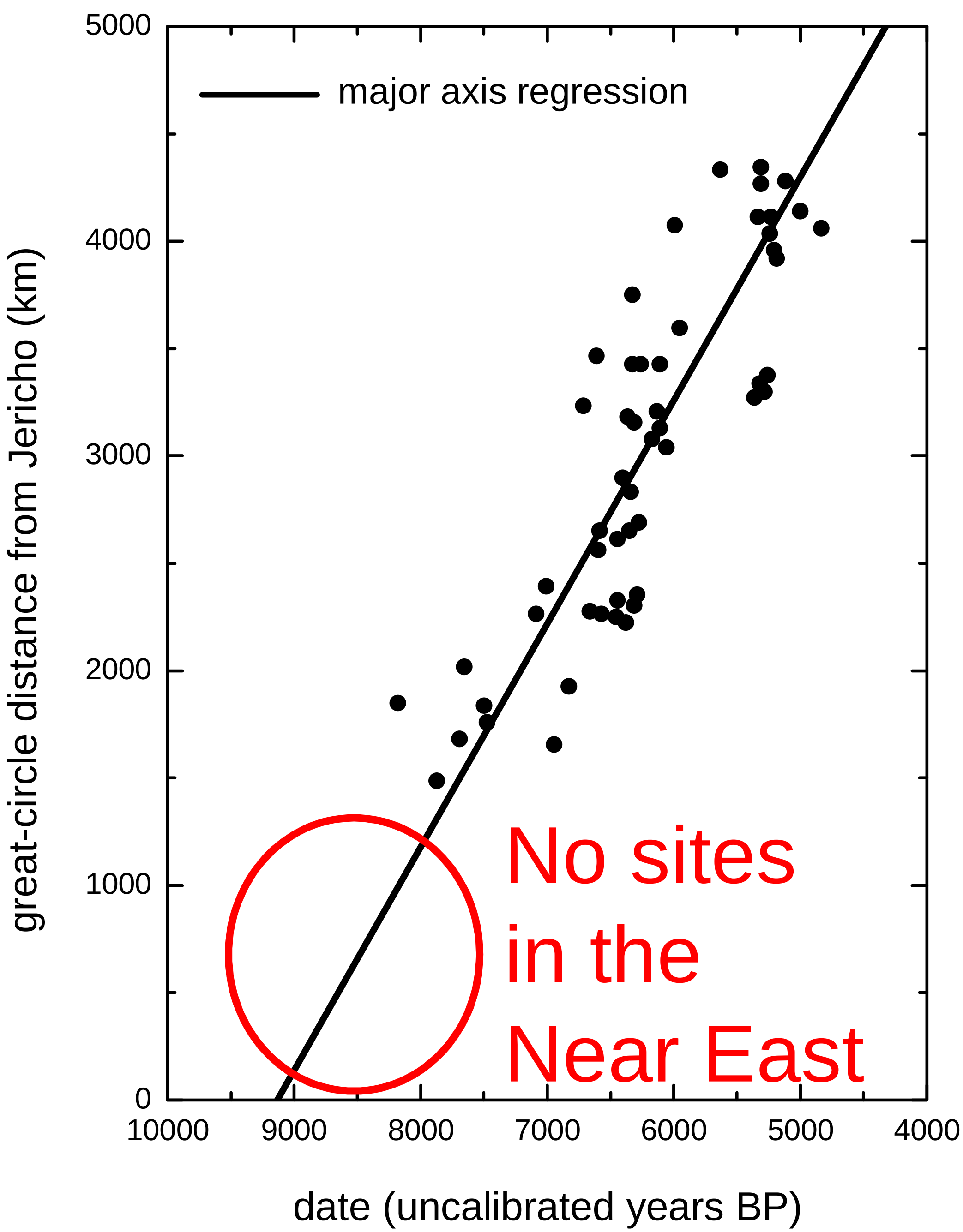
1- Demic model: it assumes that it was mainly driven by the spread of farming populations.

2- Cultural model: it assumes that it was mainly a spread of ideas (transmission of plants, animals and knowledge from farmers to hunter-gatherers).

Can demic and/or cultural models describe the data?

Plan of the talk

- 1) Data in Europe
- 2) Demic, cultural and demic-cultural models
- 3) Cultural vs demic diffusion in Europe
- 4) “ “ “ “ in southern Africa
- 5) Local features (Europe)
- 6) Role of drift in cultural evolution (Europe)



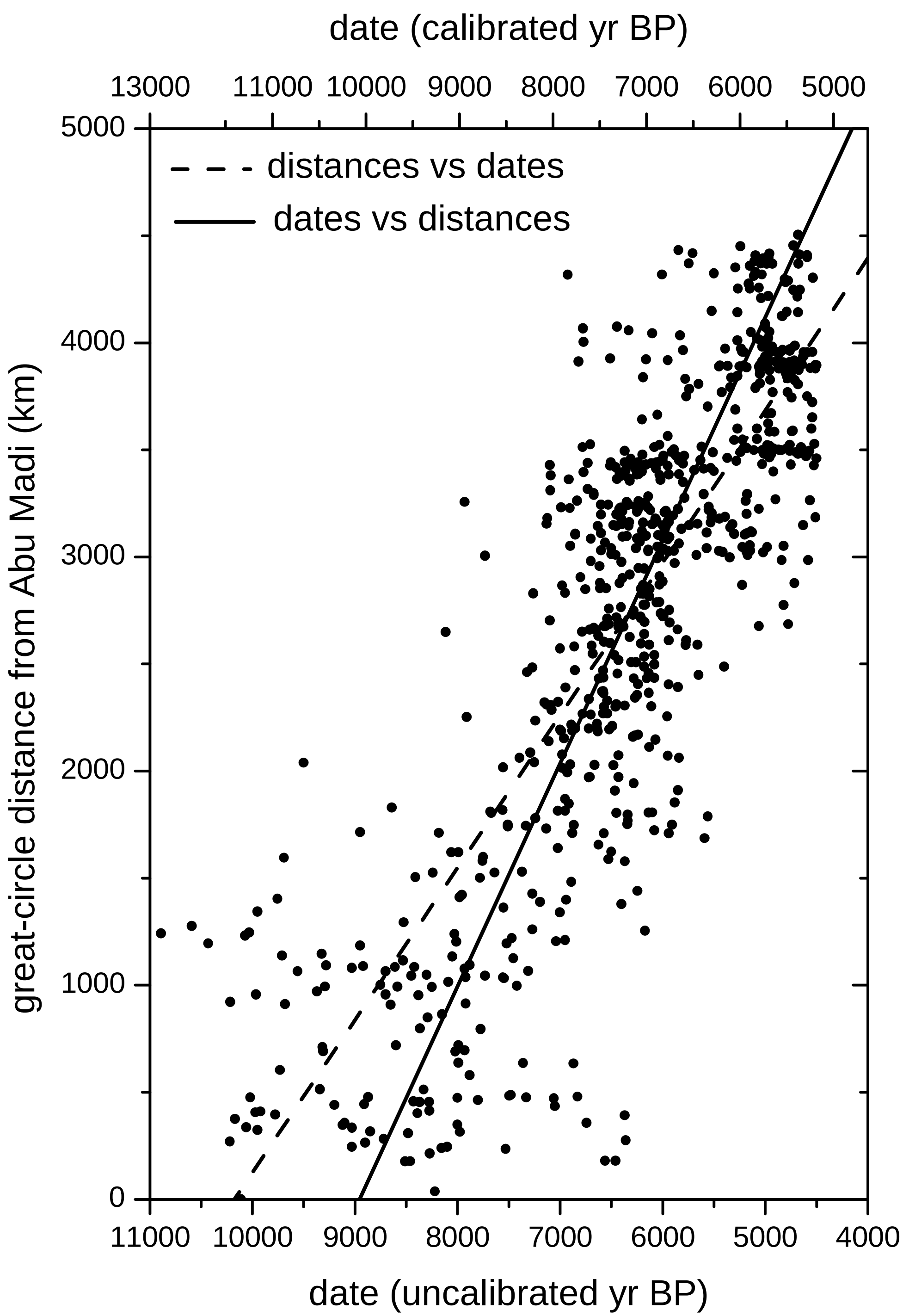
Ammerman & Cavalli-Sforza (1971)

53 sites in Europe

speed = 1.0 km/yr

(0.8-1.2 km/yr from 2 regressions)

r = 0.89 (Jericho, highest-*r* origin)



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

735 sites in Europe & the Near East

speed = 1.0 km/yr

(0.6-1.3 km/yr)

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

Ammerman & Cavalli-Sforza (1973)

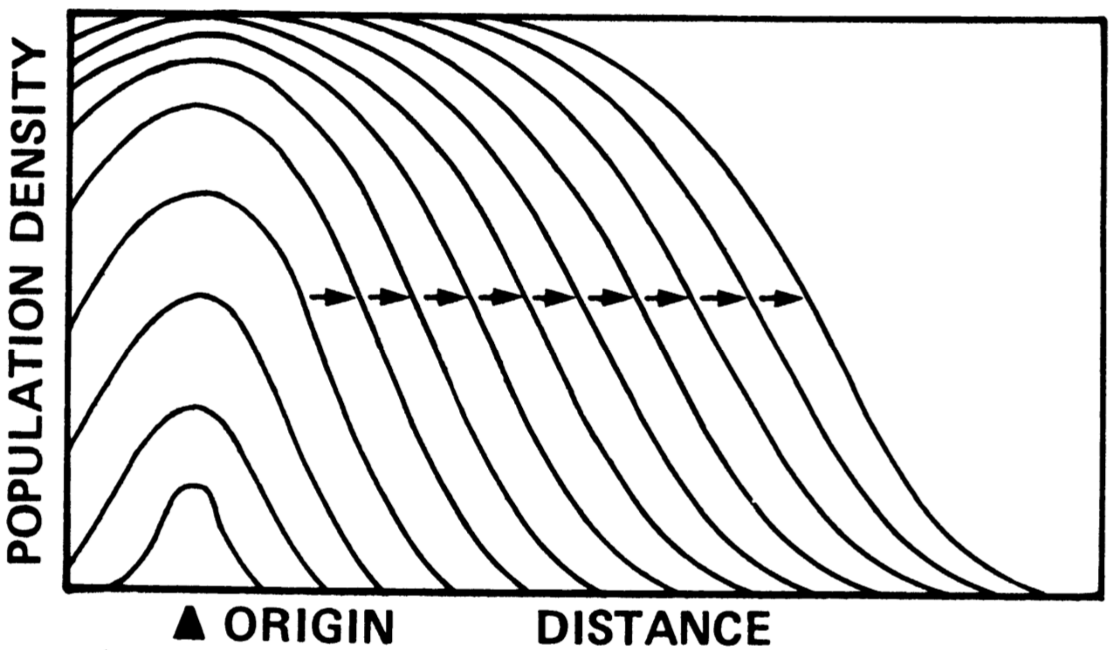


FIGURE 5.2. Fisher's model of a population wave of advance. This graphic representation shows the rise in local population density expected with increasing distance

Wave of Advance
demic model

$$v_{Fisher} = \sqrt{\frac{r\,m}{T}}$$

Preindustrial farmers:

$$\left.\begin{aligned} \text{Reproduction: } & r = 0.032 \text{ yr}^{-1} \\ \text{Mobility: } & m = 1544 \text{ km}^2 \\ \text{Generation time: } & T = 25 \text{ yr} \end{aligned}\right\} \rightarrow v_{Fisher} = 1.4 \text{ km/yr}$$

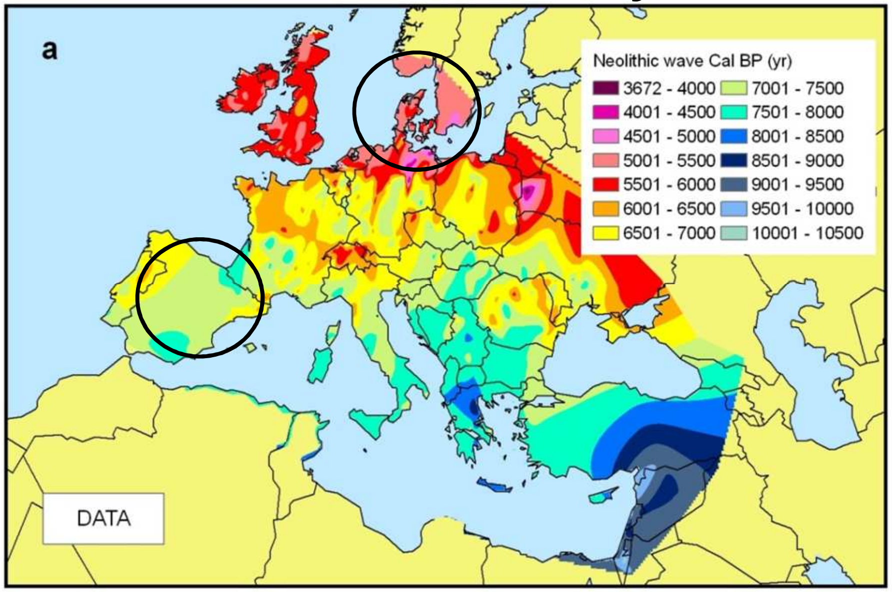
Time-delayed demic model

It takes into account that children spend some time with their parents before becoming adults and dispersing

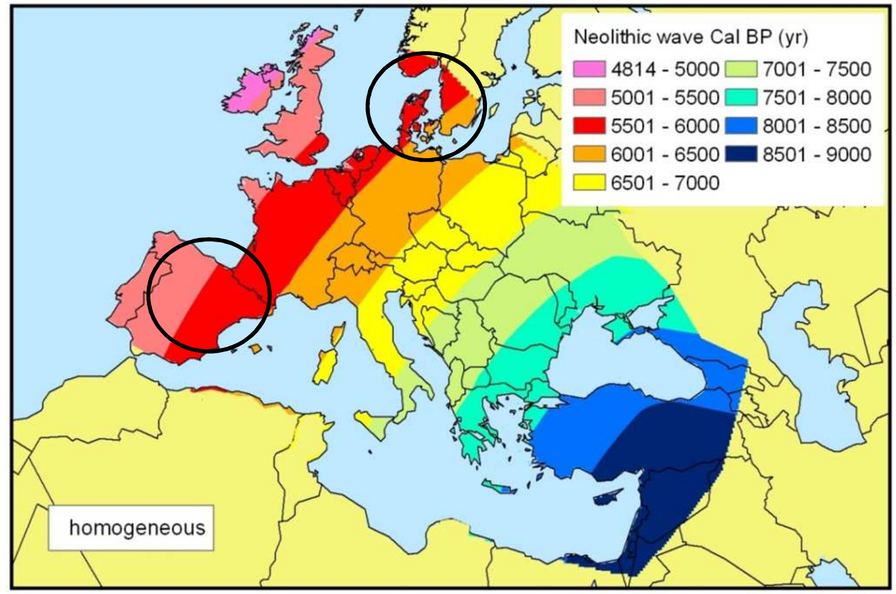
$$v = \frac{v_{Fisher}}{1 + \frac{r\,T}{2}} = 1.0\ \text{km/yr} \rightarrow 40\%$$

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

DATA → 1 km/yr



HOMOGENEOUS MODEL → 1 km/yr



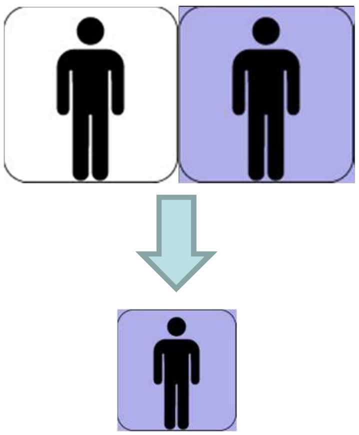
The homogeneous model agrees with the <u>average</u> observed speed but not with local features (circles).

Non-homogeneous models
(not explained in this talk)
can improve the agreement

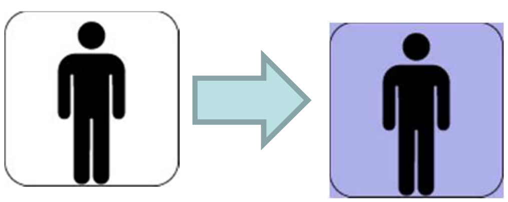
Fort, Pujol & vander Linden, *Amer. Antiq.* 2012
Isern, Fort & vander Linden, *PLoS One* 2012

Cultural models

Cultural transmission takes 2 forms



1) **Vertical** transmission is due to interbreeding between farmers and hunter-gatherers



2) **Horizontal/oblique** transmission is due to acculturation (copying)

Vertical transmission

Cavalli-Sforza & Feldman (1979)

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

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

η = interbreeding parameter ($P_H \ll P_F \rightarrow$ max. η =1)

This effect on the speed seems **small**

(Fort, *Phys. Rev. E*, 2011)

Let us consider horizontal/oblique transmission

Horizontal/oblique transmission

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

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

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

f = intensity of cultural transmission

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

Lotka-Volterra eqs. ($P'_F = P_F + \eta P_F P_H$) are <u>not</u> realistic as:

- they are not derived from cultural transmission theory
- they yield, e.g.: if $P_H \rightarrow \infty$, then $\frac{P'_F - P_F}{P_F} \rightarrow \infty$!!

Fort (*PNAS* 2012)

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

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

if $P_H \gg P_F$, then

$\frac{P_F' - P_F}{P_F} = C$ 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 $C = \frac{f}{\gamma}$.

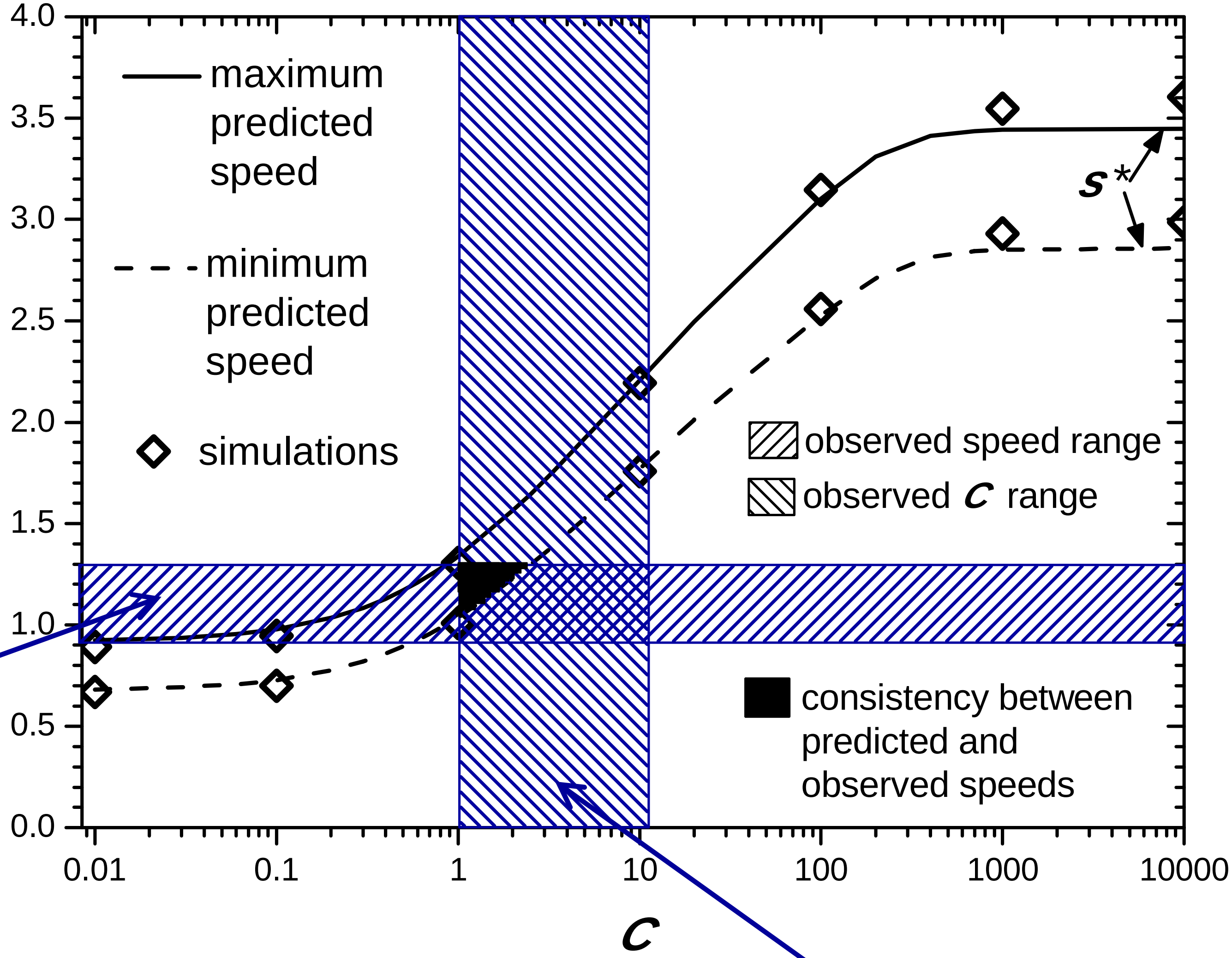
Demic-cultural model with horizontal/oblique transmission

2 ways to compute the front speed, same results:

1) Using equations for the front speed
(not shown here)

2) Using simulations on a grid
Simulation steps:
2.1) reproduction (logistic)
2.2) cultural transmission
2.3) dispersal (distance kernel)

Effect of horizontal/oblique transmission on the front speed



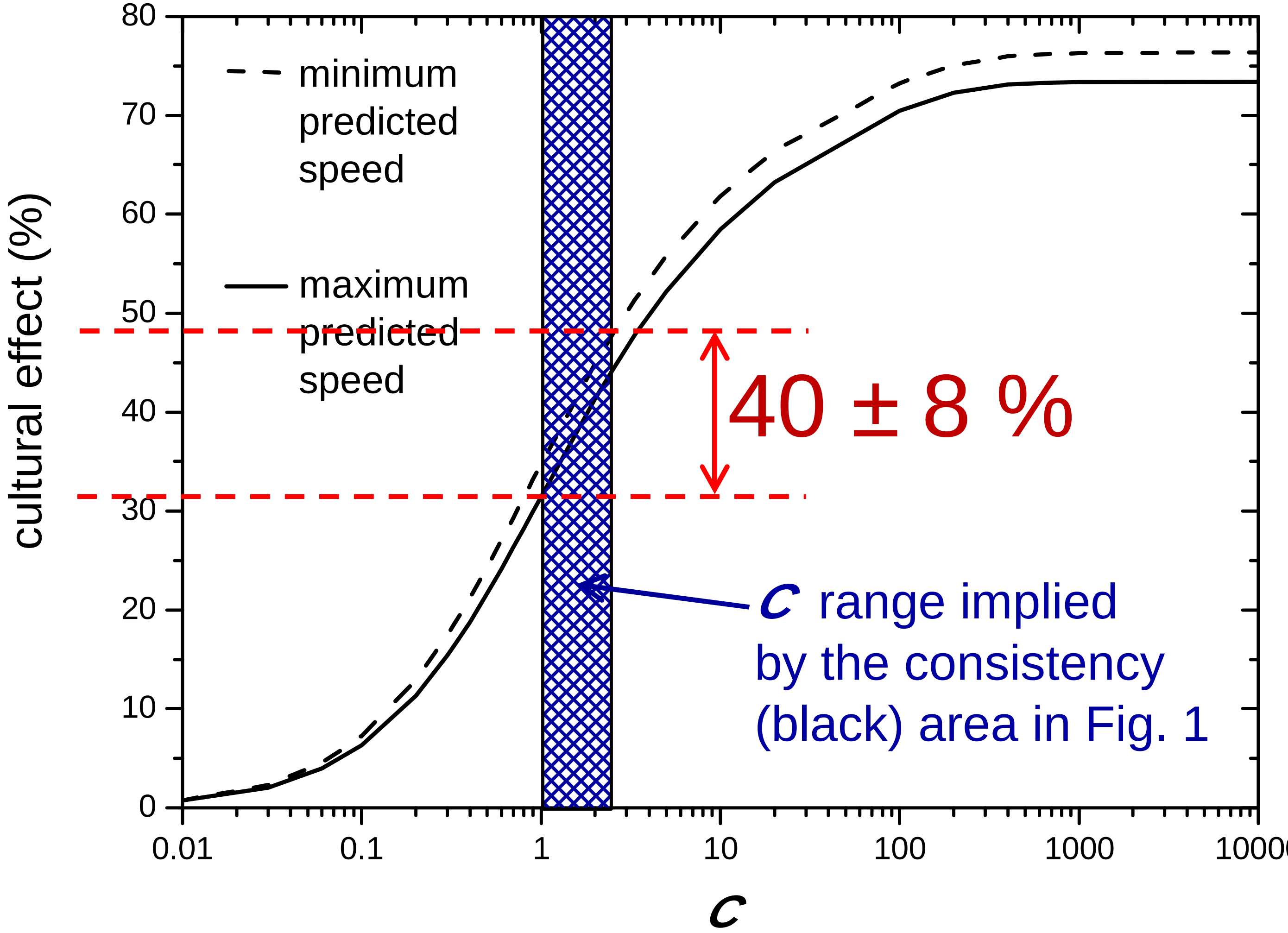
Dates versus distances (great circles & shortest paths)

Ache hunter-gatherers (Paraguay)

Fort, *PNAS* (2012)

Effect of cultural transmission

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



Fort, *PNAS* (2012)

Effect of cultural transmission on the Neolithic spread

Genetics: no clear conclusion
(depends strongly on the genes, populations demographic models…)

Archaeology:

40 % cultural
60% demic

Cultural diffusion cannot be neglected, but demic diffusion seems more important

Frequency-dependent (conformist) effect

This is a more refined model, see e.g.:

· Boyd & Richerson (1985)

· Kandler & Steele (2009)

· Henrich (2001) $\rightarrow$ it explains the slow initial growth of innovation S-shaped curves

$$\begin{cases} P_F' = P_F + \dfrac{P_F P_H}{P_F + \gamma P_H}\left(f + h\left[2\dfrac{P_F}{P_F + P_H} - 1\right]\right) \\ P_H' = P_H - \dfrac{P_F P_H}{P_F + \gamma P_H}\left(f + h\left[2\dfrac{P_F}{P_F + P_H} - 1\right]\right) \end{cases}$$

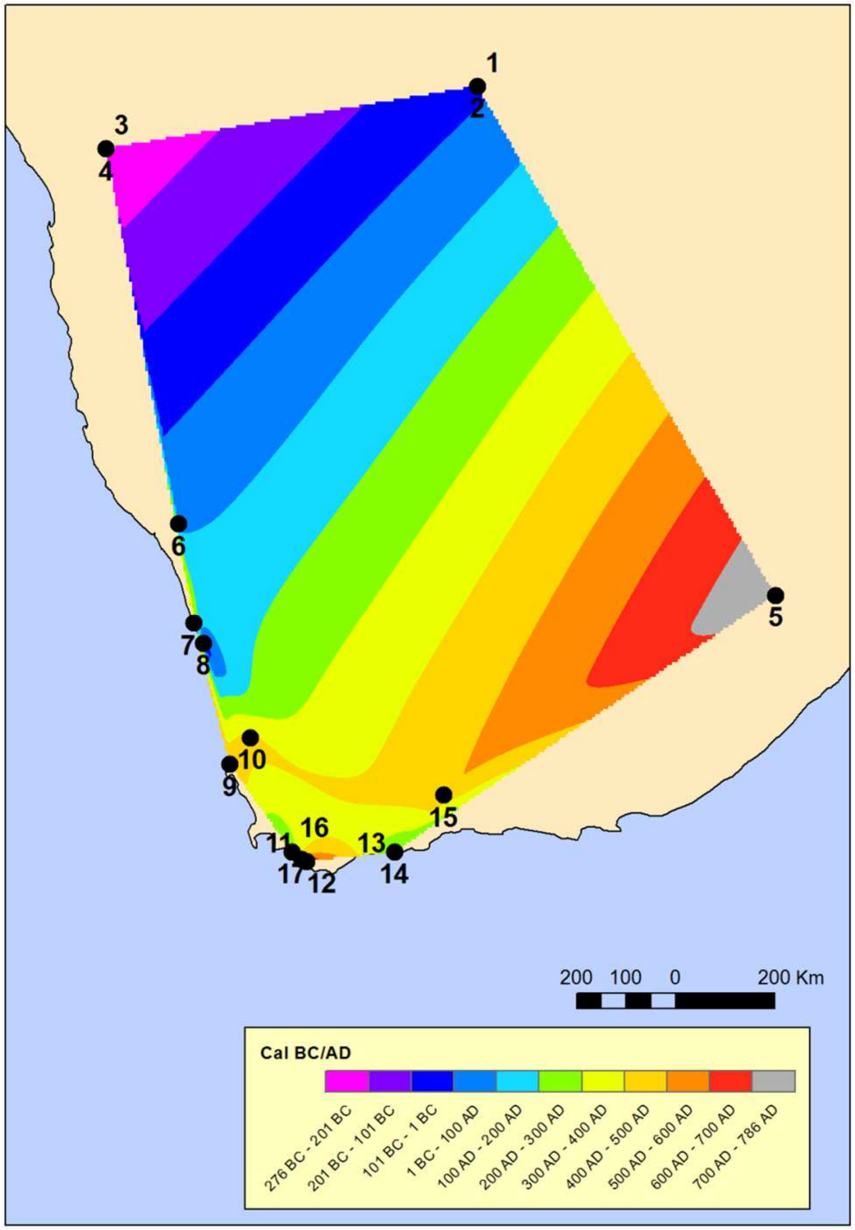
$h = 0 \rightarrow$ previous model.

· If $u = P_F / (P_F + P_H) > 1/2 \rightarrow$ positively-biased,

· If $u < 1/2 \rightarrow$ negatively-biased.

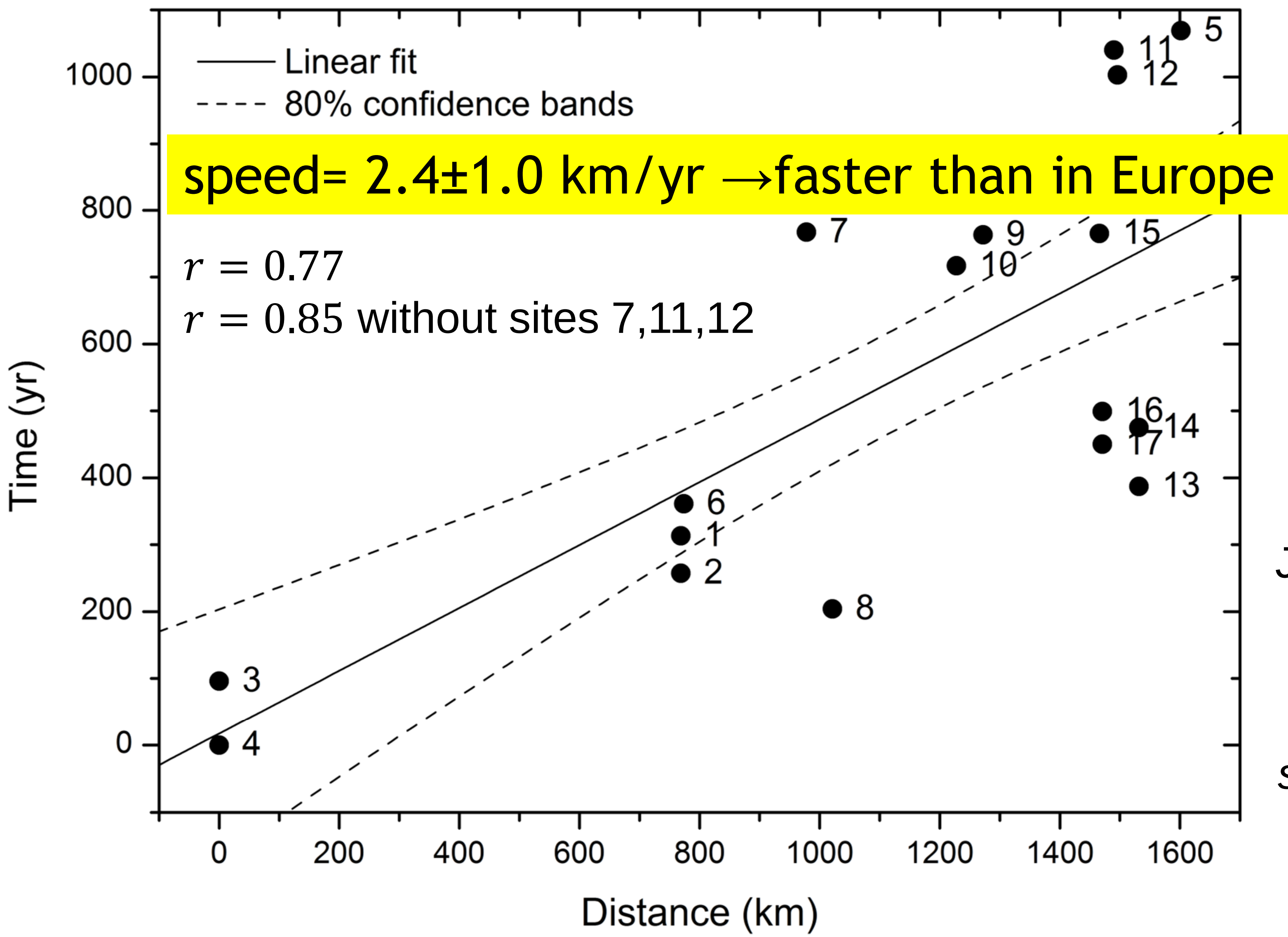
Exactly the same results as for the former model.

The Neolithic transition in southern Africa



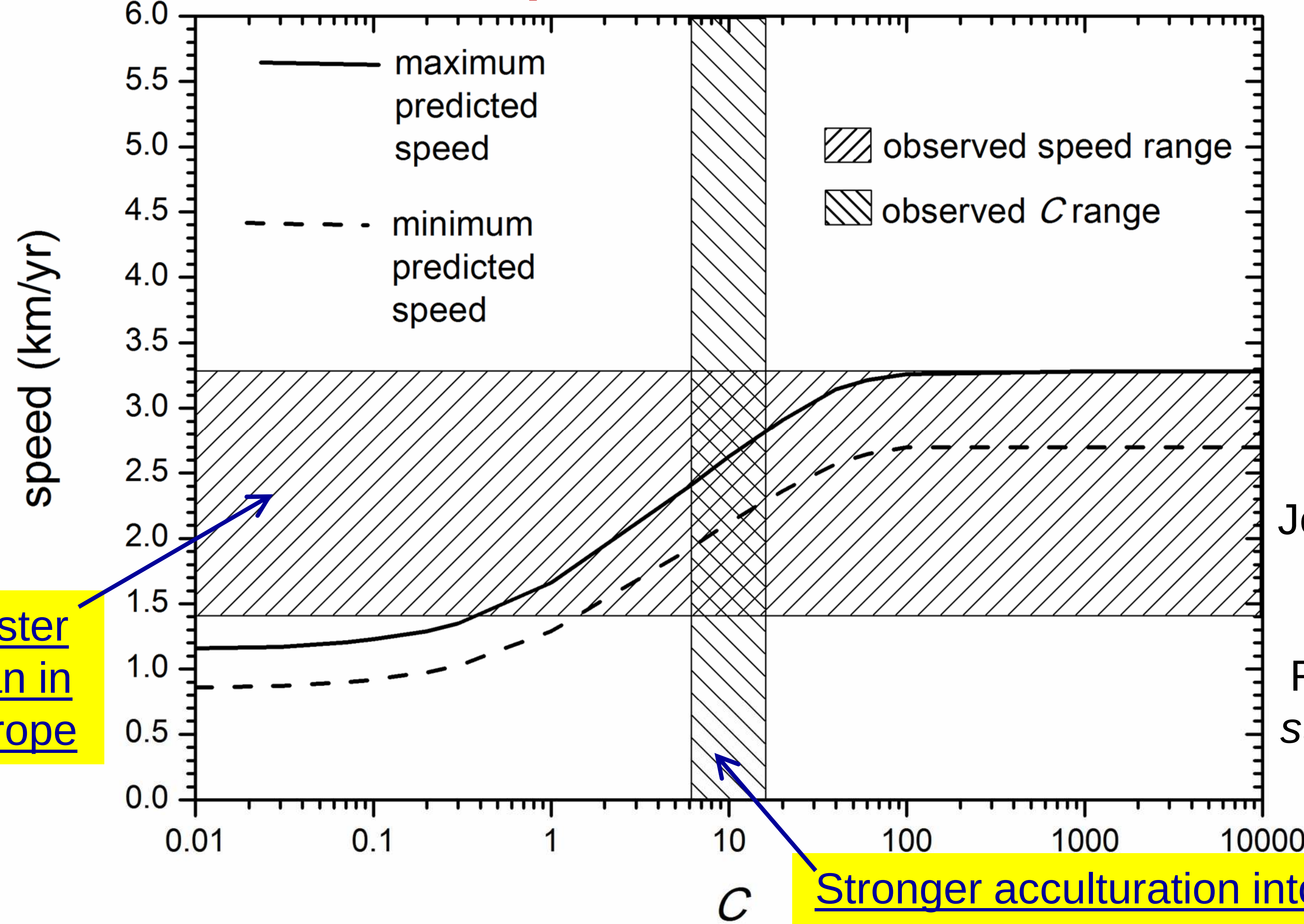
Jerardino, Fort, Isern, Rondelli, *submitted* (2014)

The Neolithic transition <u>in southern Africa</u>



Jerardino, Fort, Isern, Rondelli, *submitted* (2014)

Effect of acculturation intensity *C* on the front speed <u>in southern Africa</u>



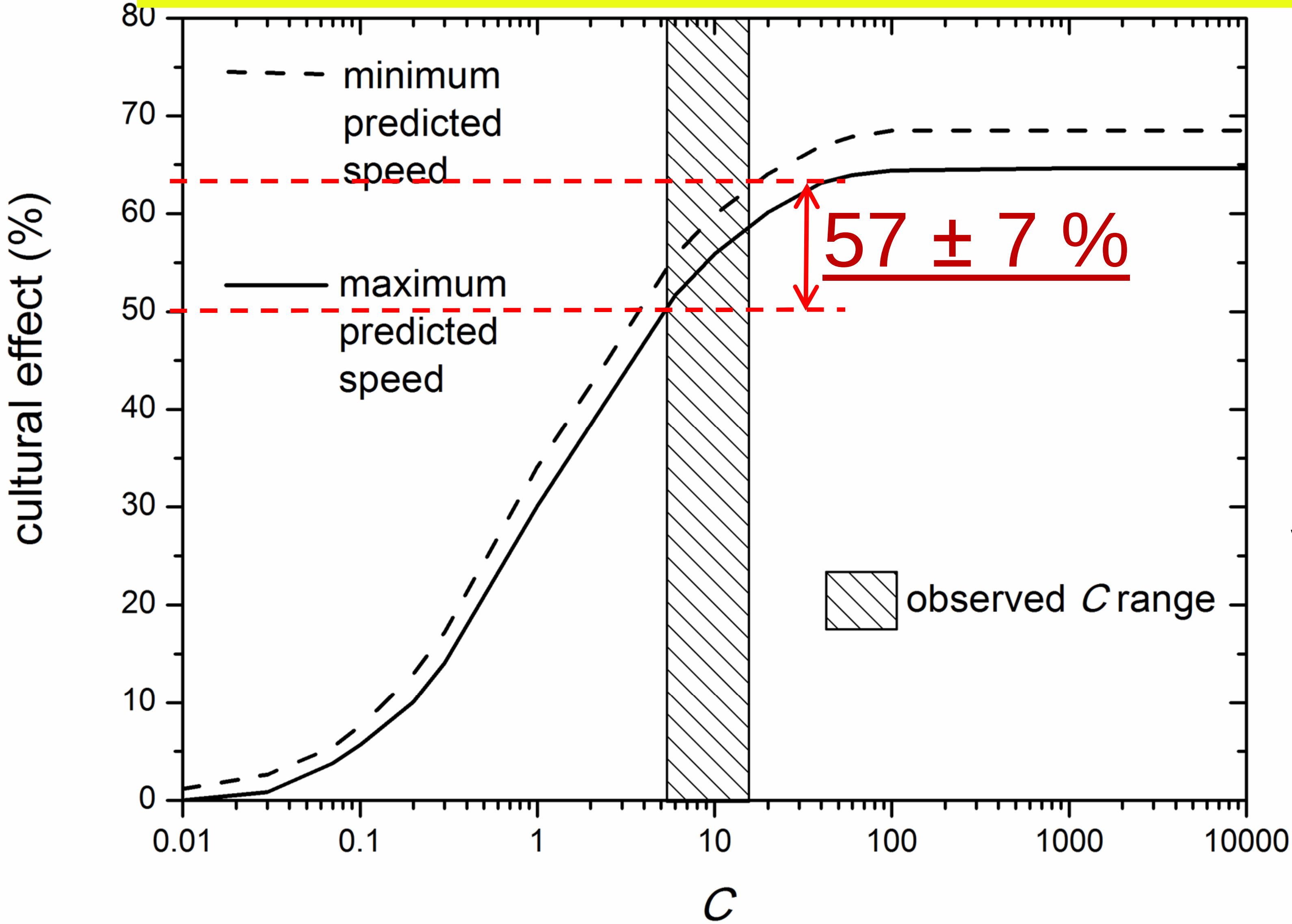
<u>Faster than in Europe</u>

<u>Stronger acculturation into herding than into farming</u>

Jerardino, Fort, Isern, Rondelli, *submitted* (2014)

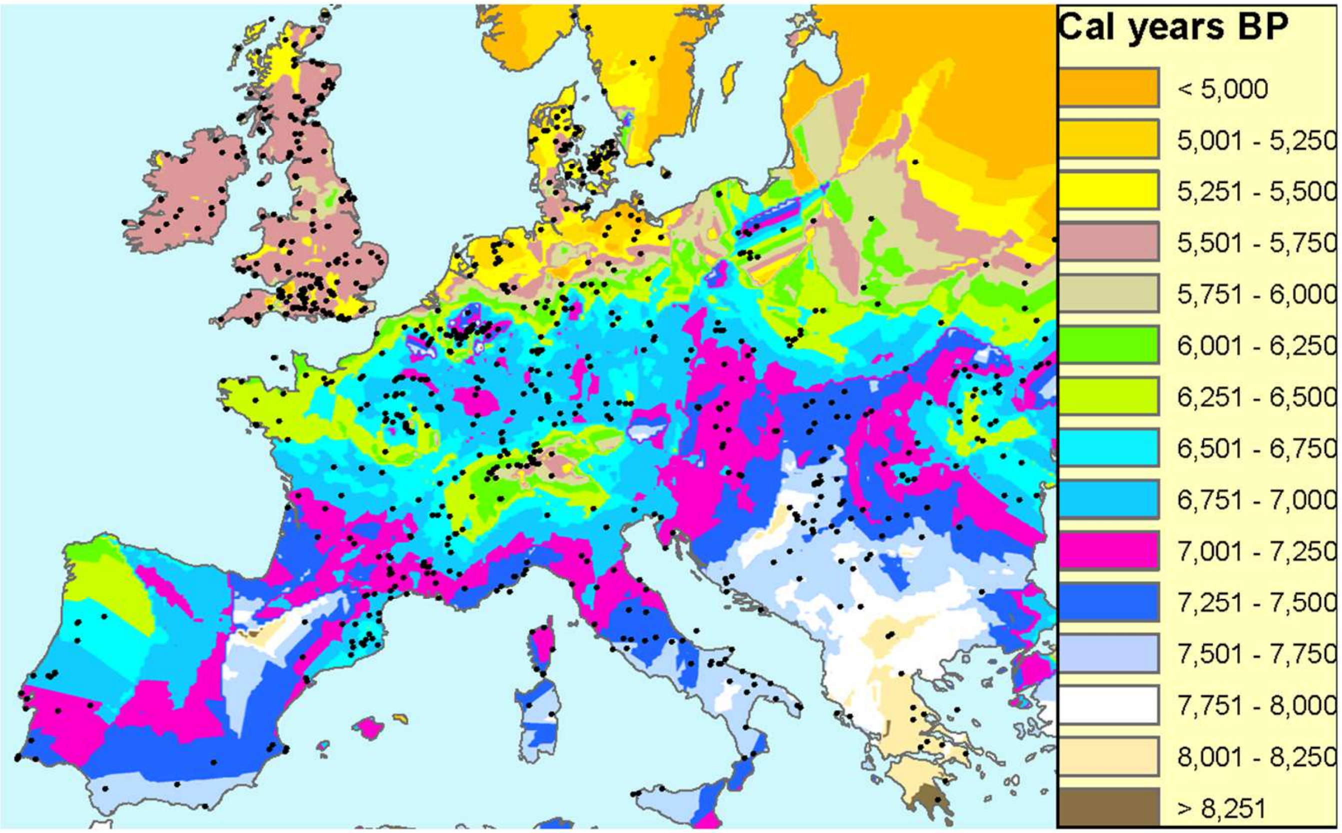
Effect of cultural diffusion in southern Africa

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

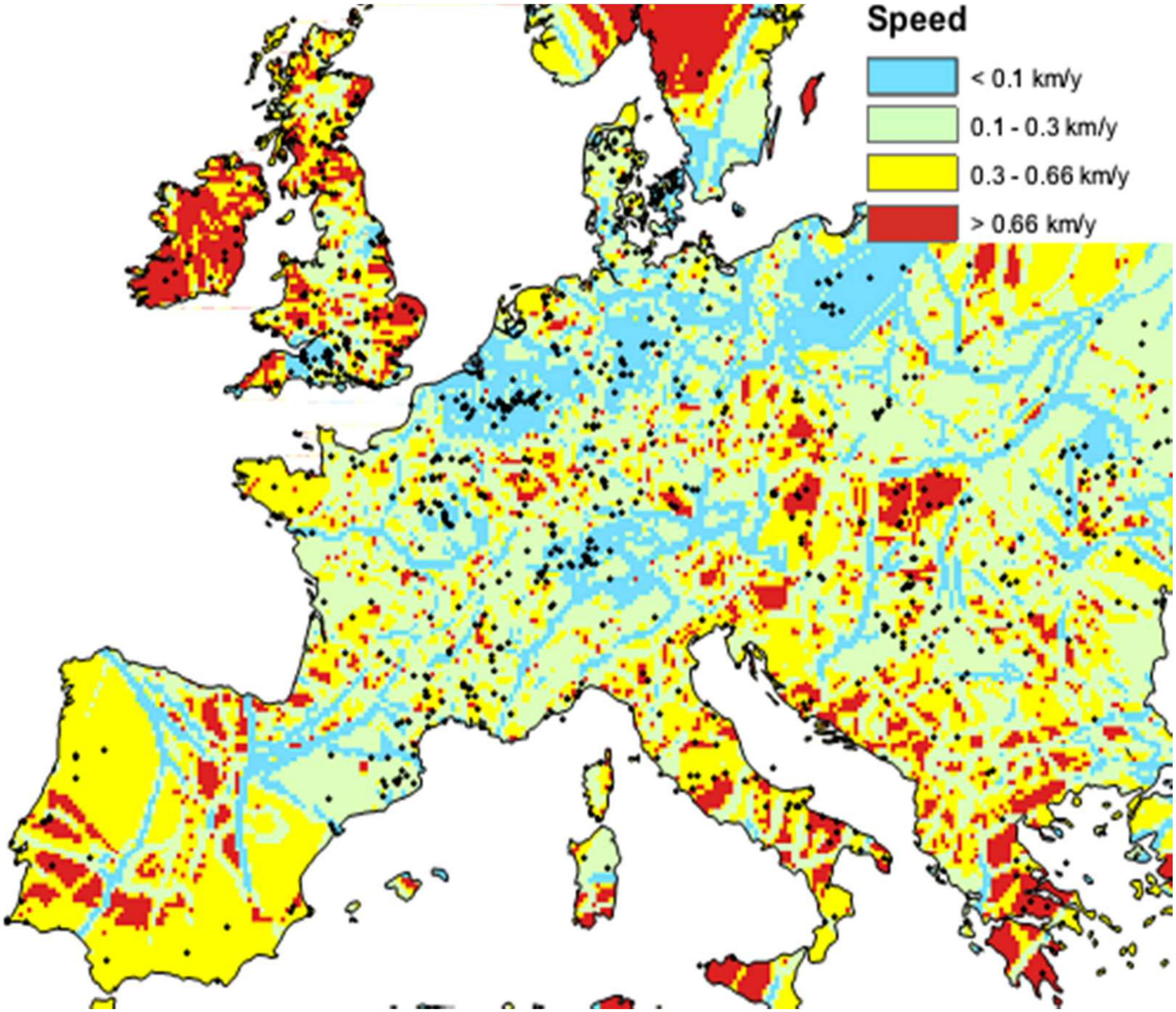


Jerardino, Fort, Isern, Rondelli, *submitted* (2014)

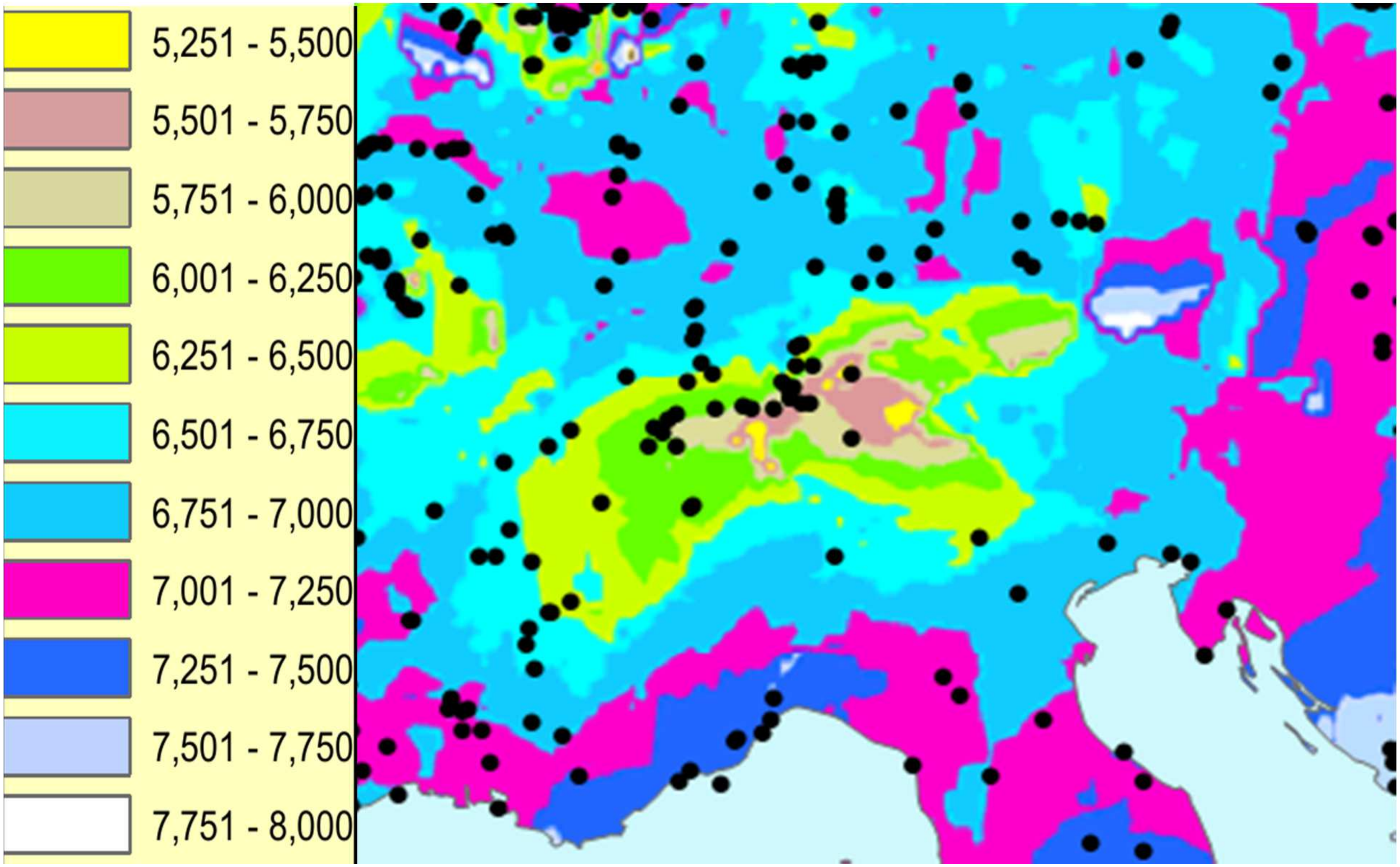
Local features in Europe



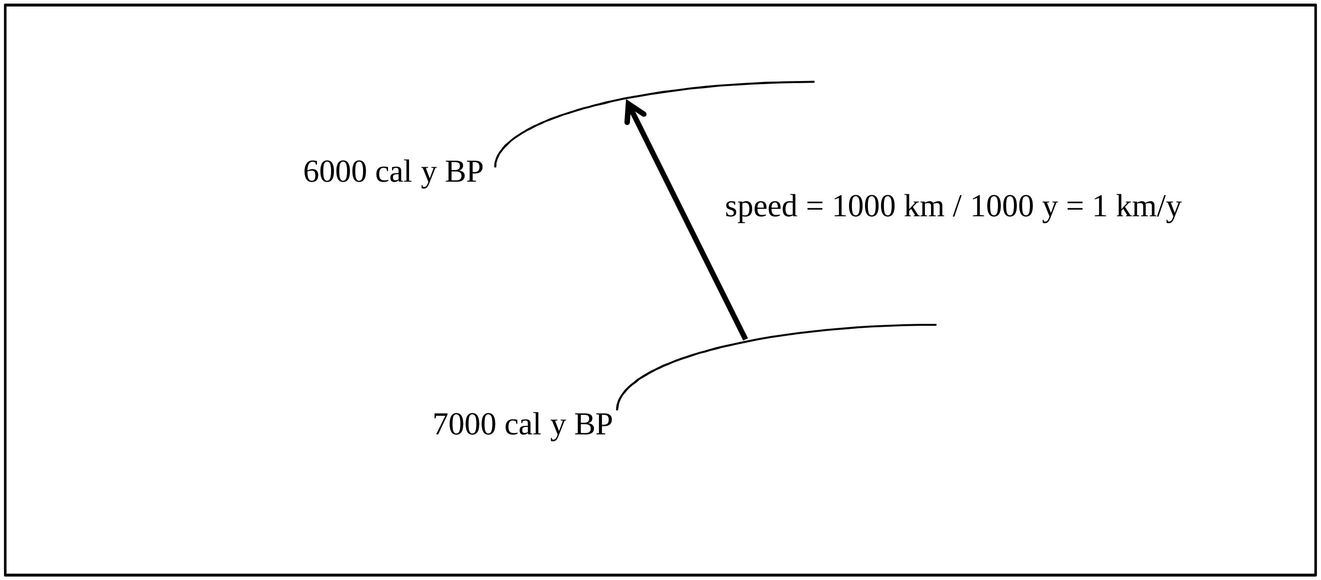
Fort,
J. R. Soc. Interface
(2014)

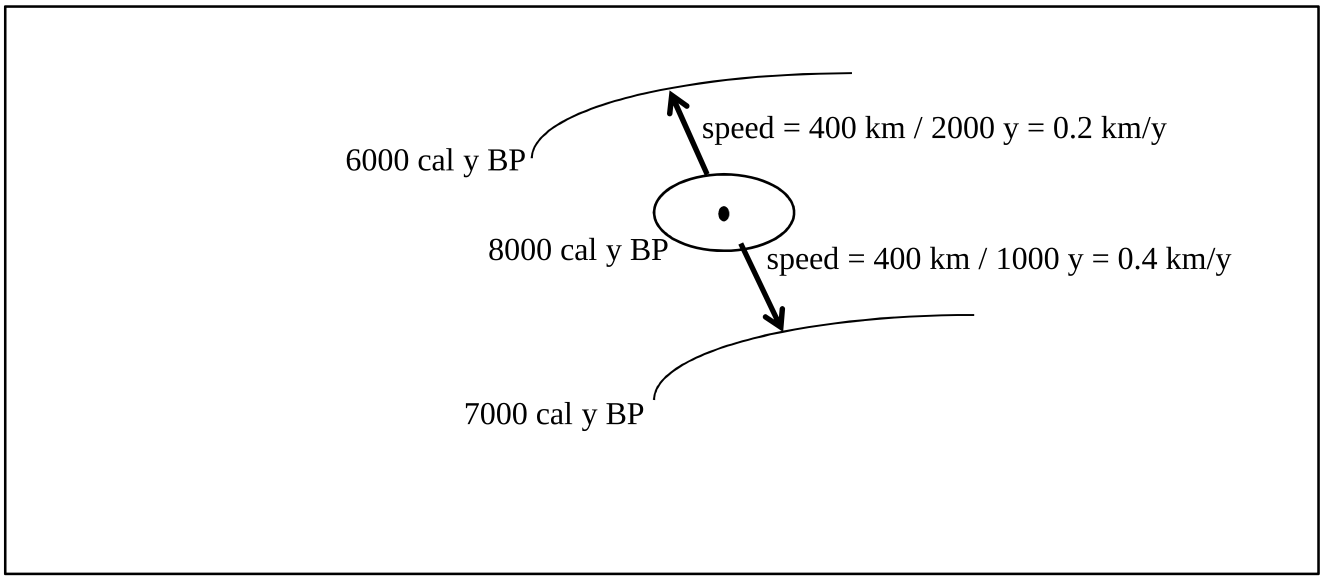


Fort,
J. R. Soc. Interface
(2014)



Fort,
J. R. Soc. Interface
(2014)





Fort,
J. R. Soc. Interface
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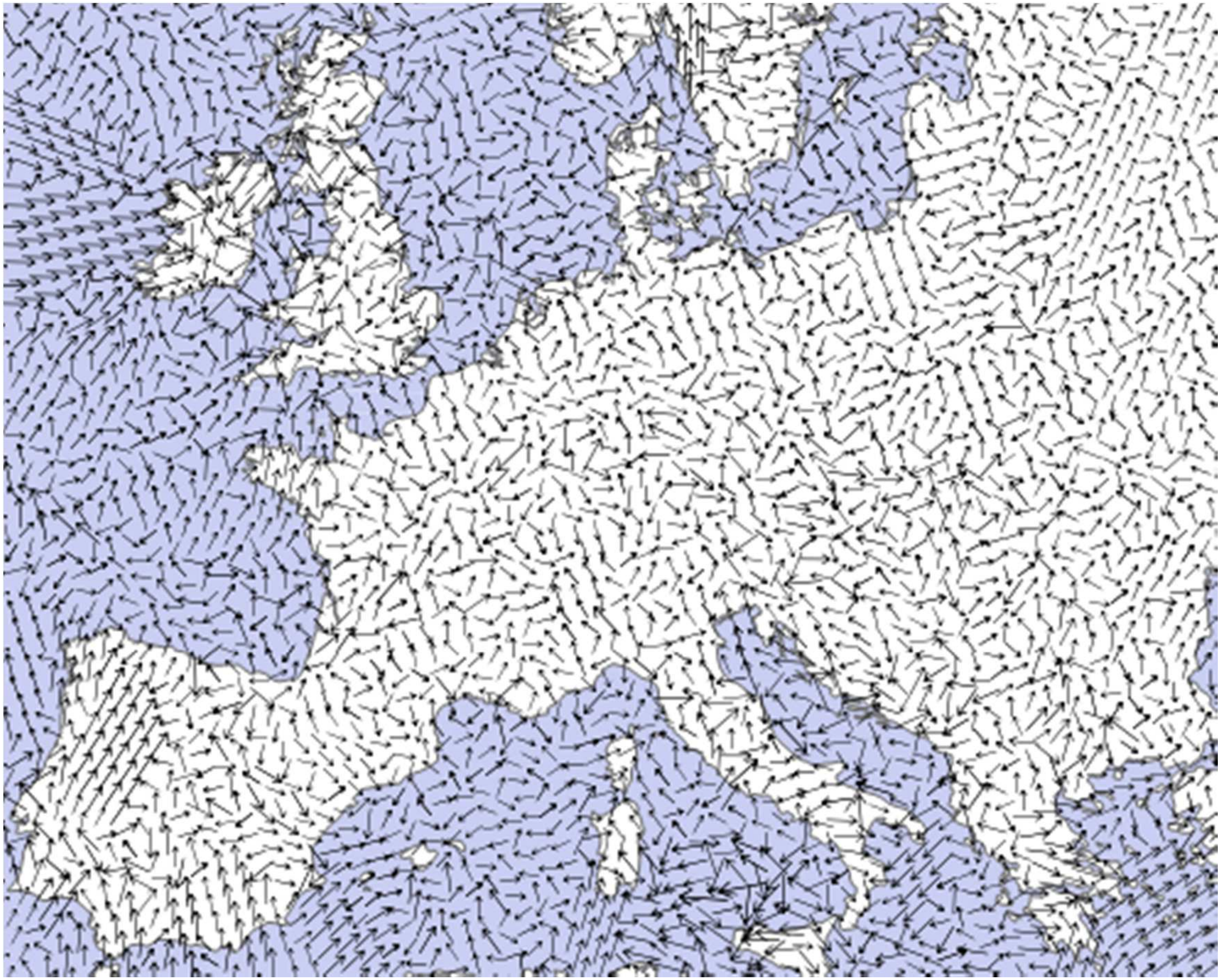

Fort,
J. R. Soc. Interface
(2014)

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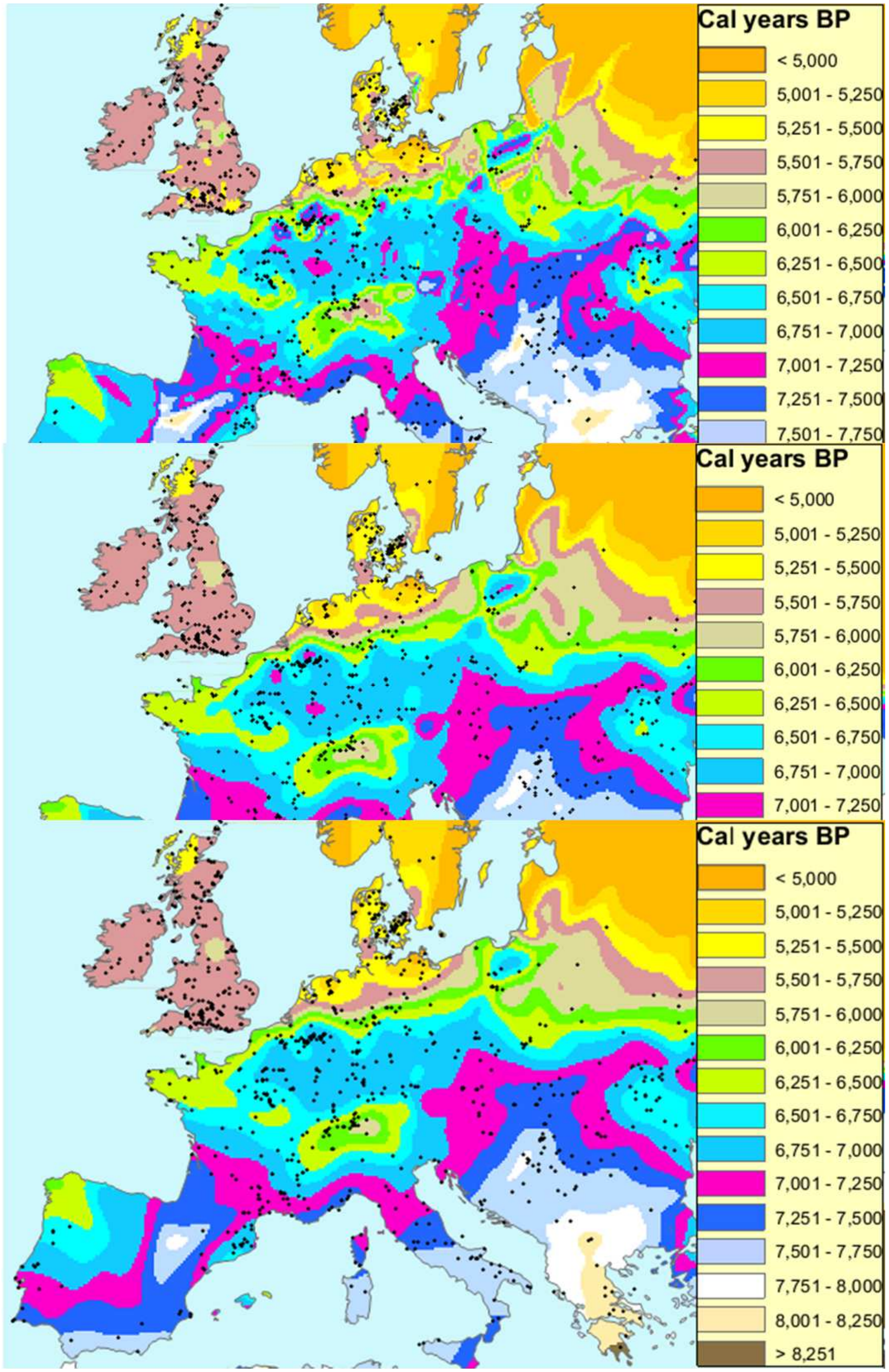
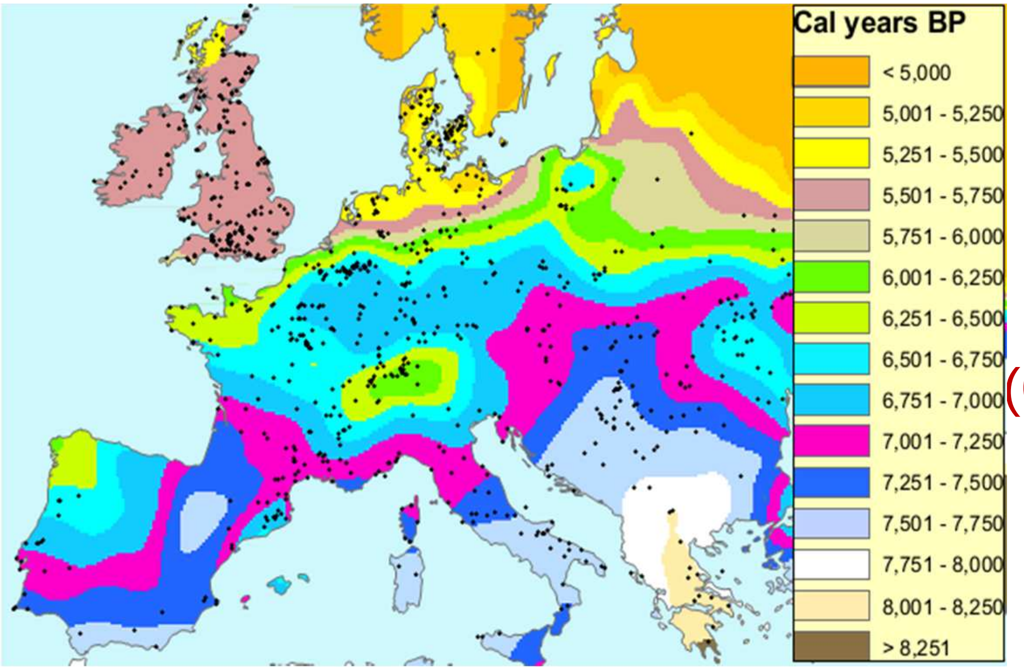


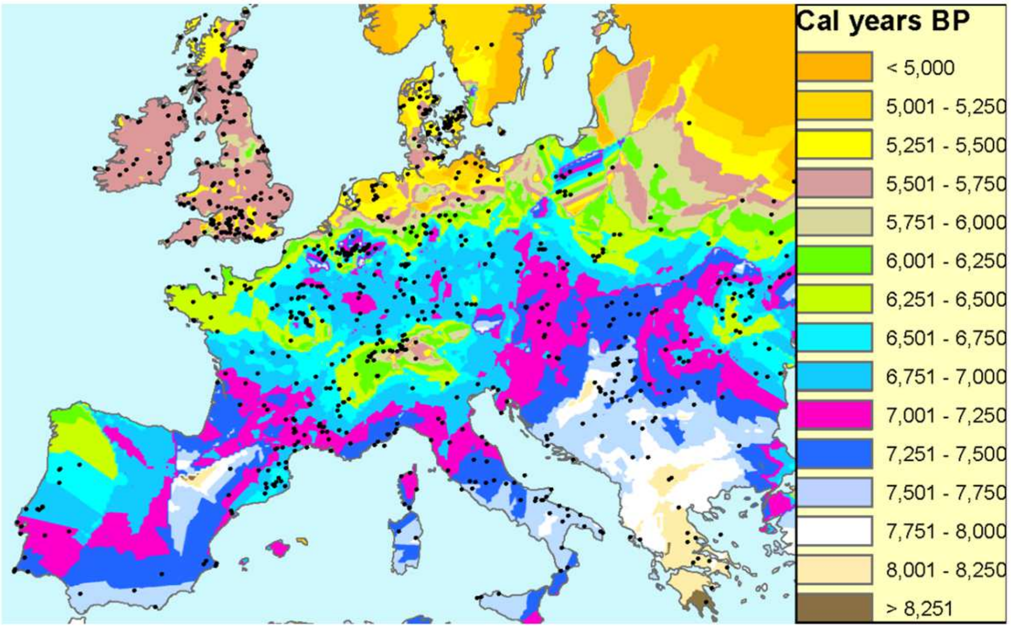
smoothing
1 time

10 times

20 times



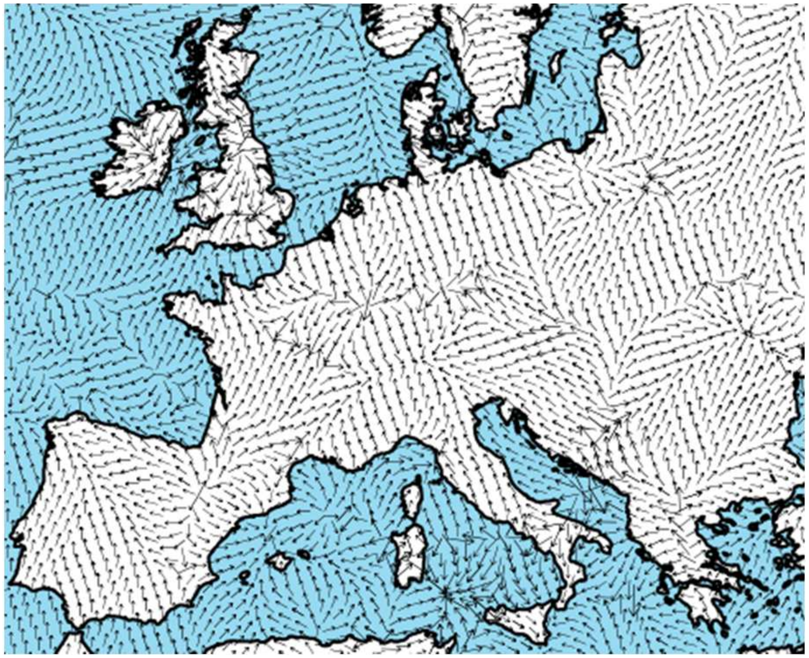
smoothing
40 times
(60 times→ same results)



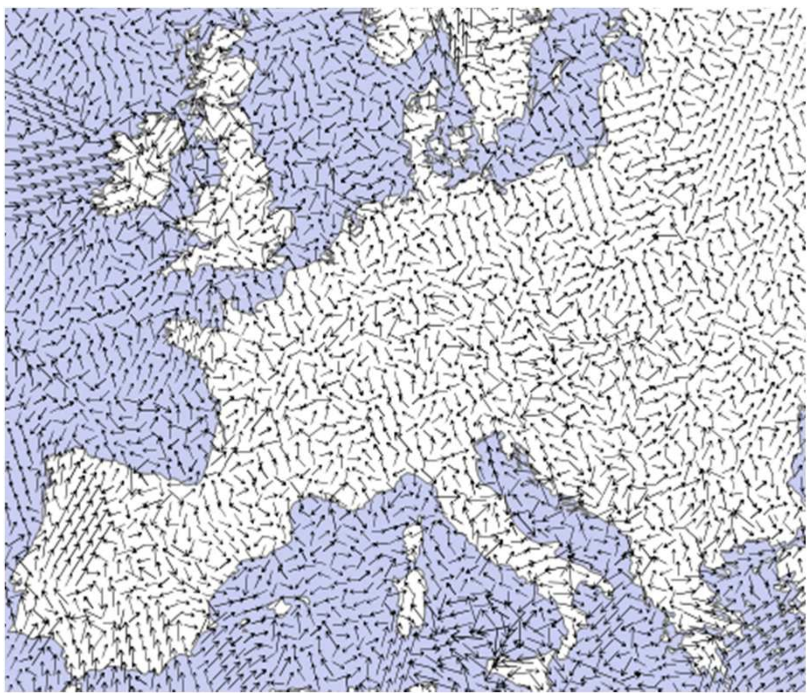
No
smoothing

Fort,
J. R. Soc. Interface
(2014)

Fig. 1

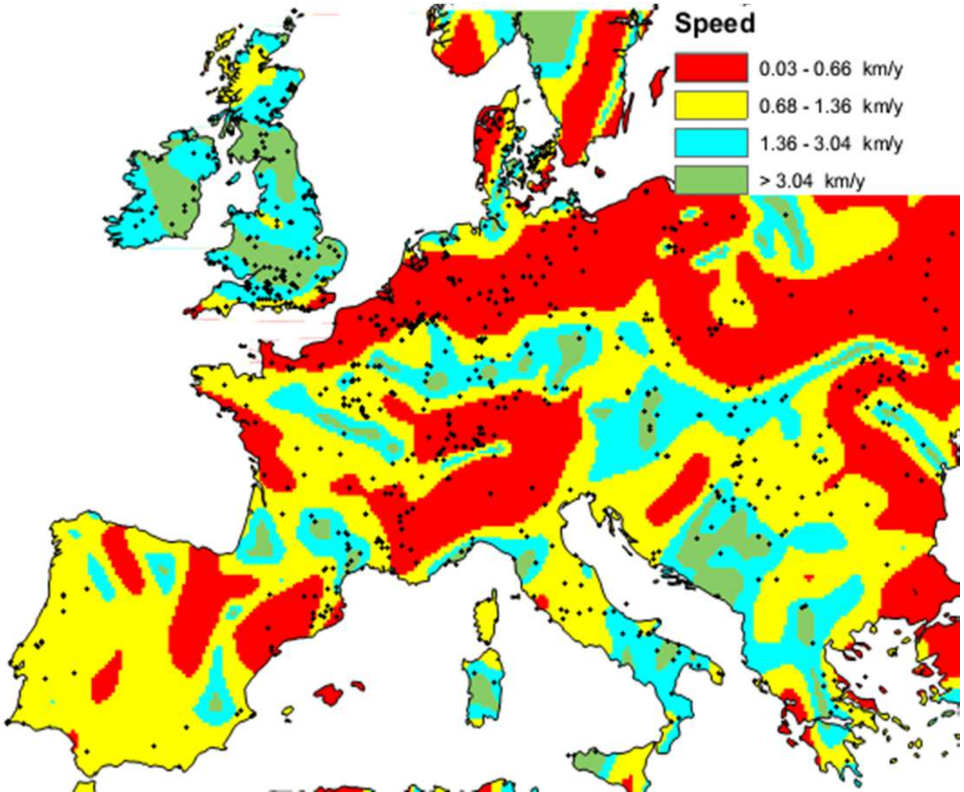


smoothing
40 times
(60 times→ same results)

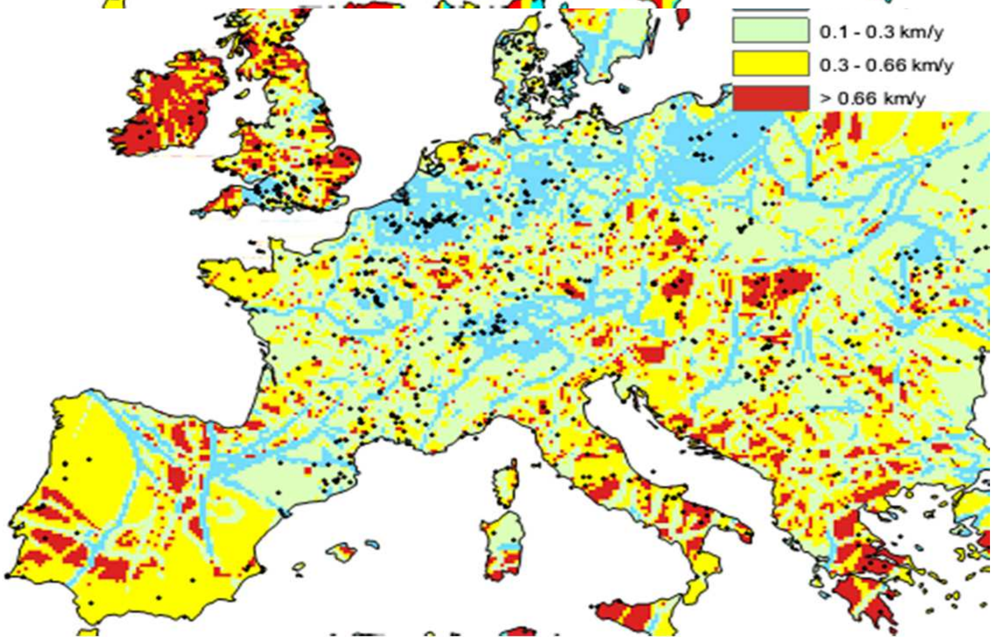


No smoothing

Fort,
J. R. Soc. Interface
(2014)



smoothing
40 times



No smoothing

Fort,
J. R. Soc. Interface
(2014)

Smoothing 40 times

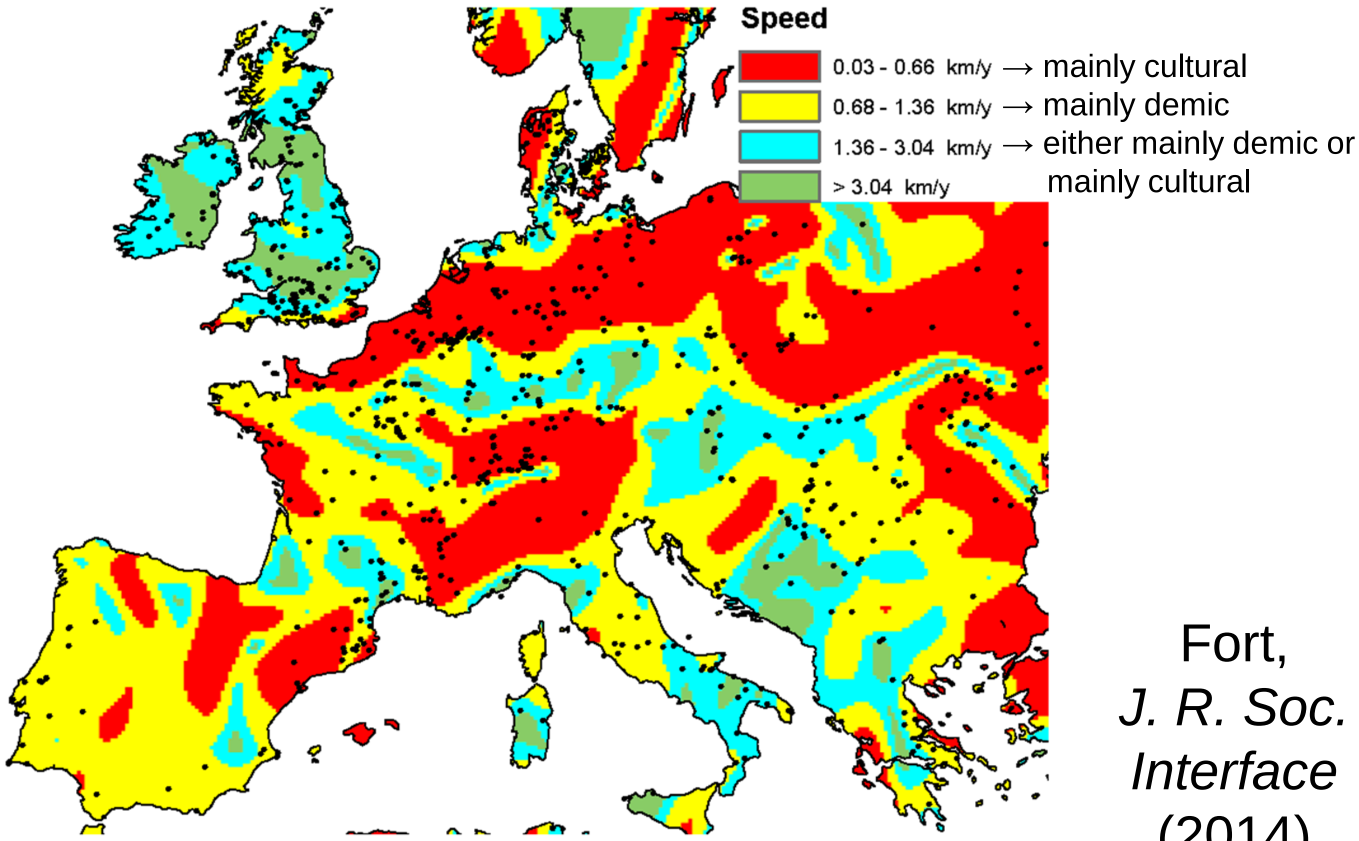


Fig. 3

Fort,
J. R. Soc. Interface
(2014)

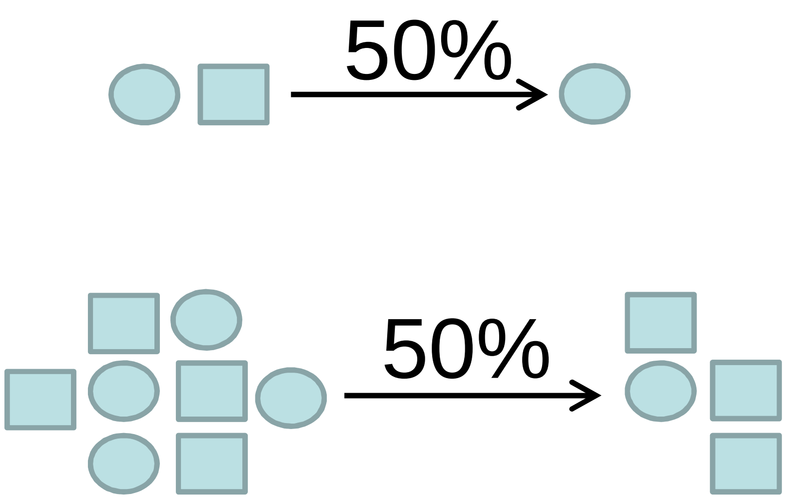
Caution: The results are approximate because the kernels are from ethnographic data, not from the Neolithic.

Prediction: Demic kernels in the mainly cultural areas (red) should be narrower than in the areas where demic diffusion was important (other).

Question: How to measure Neolithic dispersal kernels?
· Strontium isotope data (archaeology)
· Identification of parents and their children (genetics): probably more precise.

Cultural drift

Cultural drift is the change in the relative frequency of a cultural trait in a population due to random sampling



Drift may cause variants to disappear completely

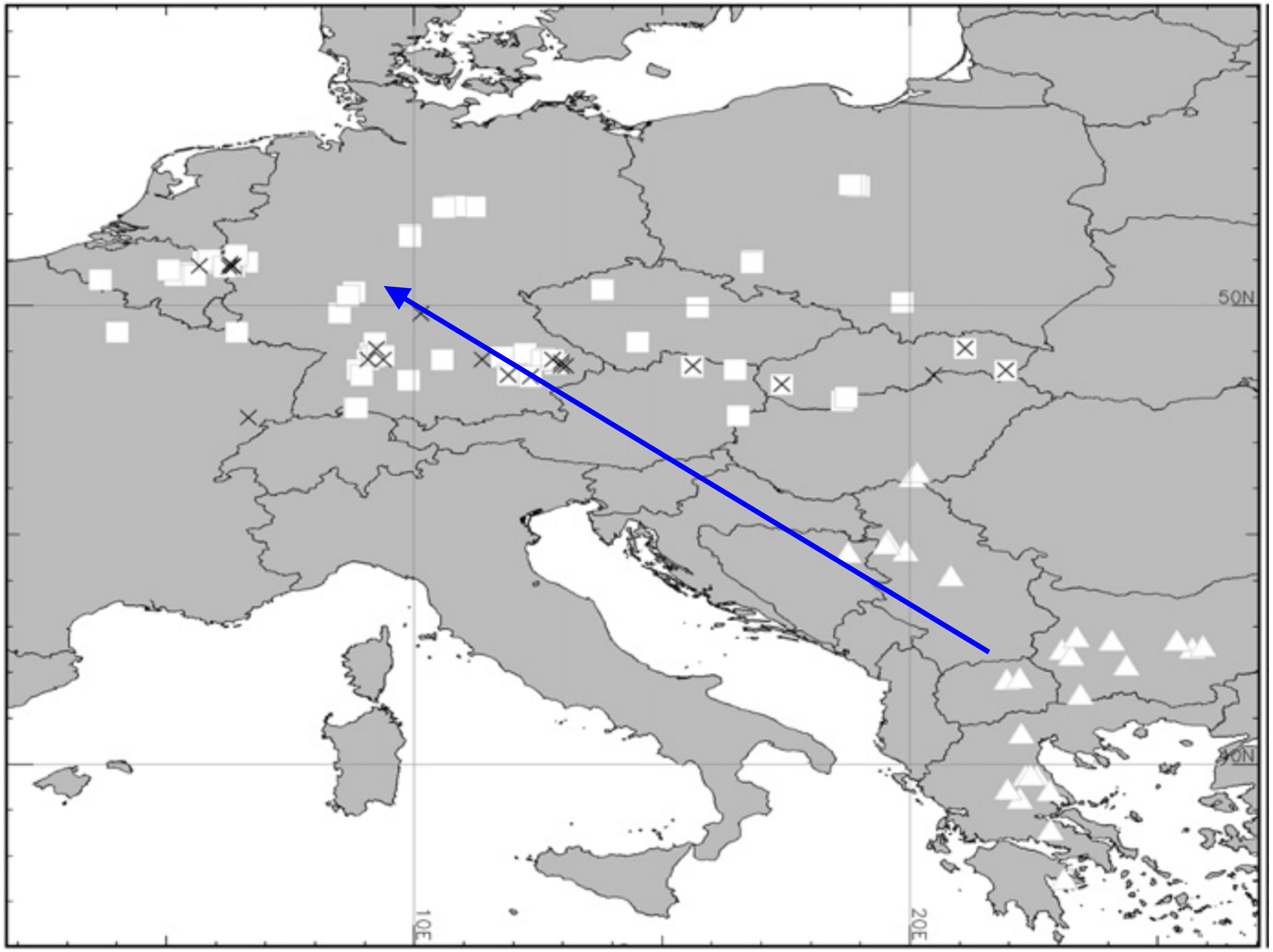
↓

This effect is expected to be **important for small population sizes**

↓

Such as on the **leading edge** (pioneering settlements) of the Neolithic front

The LBK expansion



Conolly, Colledge & Shennan (2008)

pre-LBK (triangles), LBK (squares), post-LBK (crosses)

How to quantify cultural diversity*

The cultural diversity t_F is defined as

$$t_F = \frac{1}{\sum_{i=1}^{k} p_i^2} - 1$$

Where p_i is the relative frequency of the *i*-th cultural variant (crop) in the population

*Neiman, *Amer. Antiq.* (1995)

How to compute diversity t_F

$$t_F = \frac{1}{\sum_{i=1}^{k} p_i^2} - 1$$

p_1	p_2	p_3	p_4	p_5	p_6	p_7	p_8	8 crops
1	0	0	0	0	0	0	0	$\rightarrow t_F = 0$
0.8	0.1	0.1	0	0	0	0	0	$\rightarrow t_F = 0.52$
0.3	0.2	0.2	0.1	0.1	0.1	0	0	$\rightarrow t_F = 4.0$

(-) Diversity

(+) Diversity

(-) t_F

(+) t_F

Conolly, Colledge & Shennan (2008)

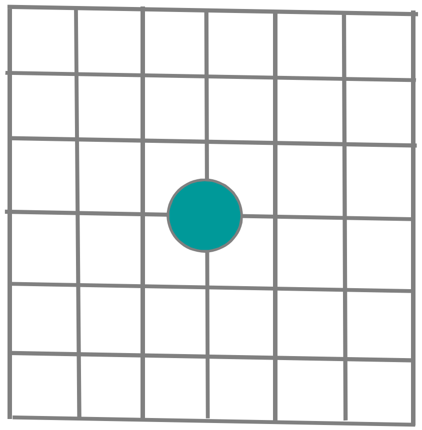
	Crop*	Taxa	p_i Pre-LBK	p_i LBK
1	Oats	Avena sp.	0.094	0.025
2	Hulled barley	Hordeum vulgare	0.18	0.075
3	Naked barley	Hordeum vulgare var. nudum	0.072	0.058
4	Pea	Pisum sativum	0.13	0.17
5	Millet	Panicum miliaceum	0.022	0.042
6	Free threshing wheat	Triticum aestivum/durum	0.11	0.046
7	Emmer	Triticum dicoccum	0.19	0.31
8	Einkorn	Triticum monococcum	0.19	0.27
	Number of sites		32	85
	Diversity (t_F)		5.3	3.7

* 8 crops less likely to have been subject to reduced productivity due to climate, etc.

Drop to t_F=3.7

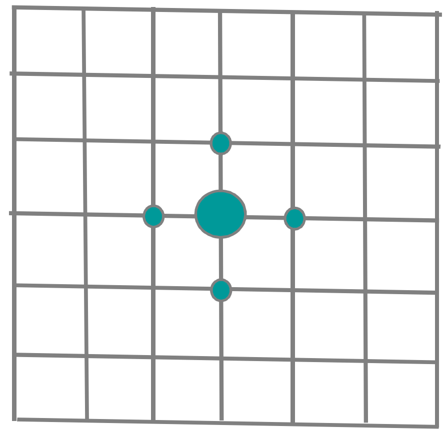
Model

(1) Initial Population



● $P(t)$

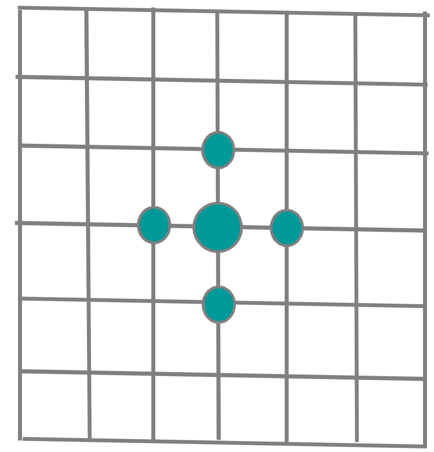
(2) Dispersal



• $P(t)\ (1-p_e)/4$

● $P(t)\ p_e$

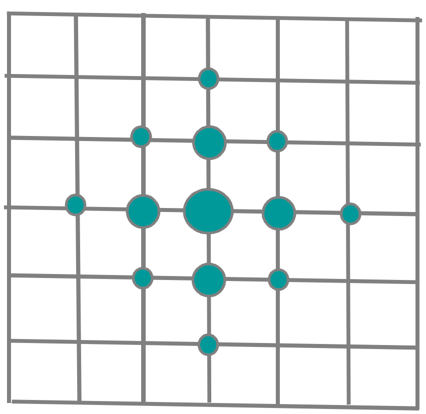
(3) Reproduction



• $Ro\ P(t)\ (1-p_e)/4$

● $Ro\ P(t)\ p_e$

(4) Dispersal

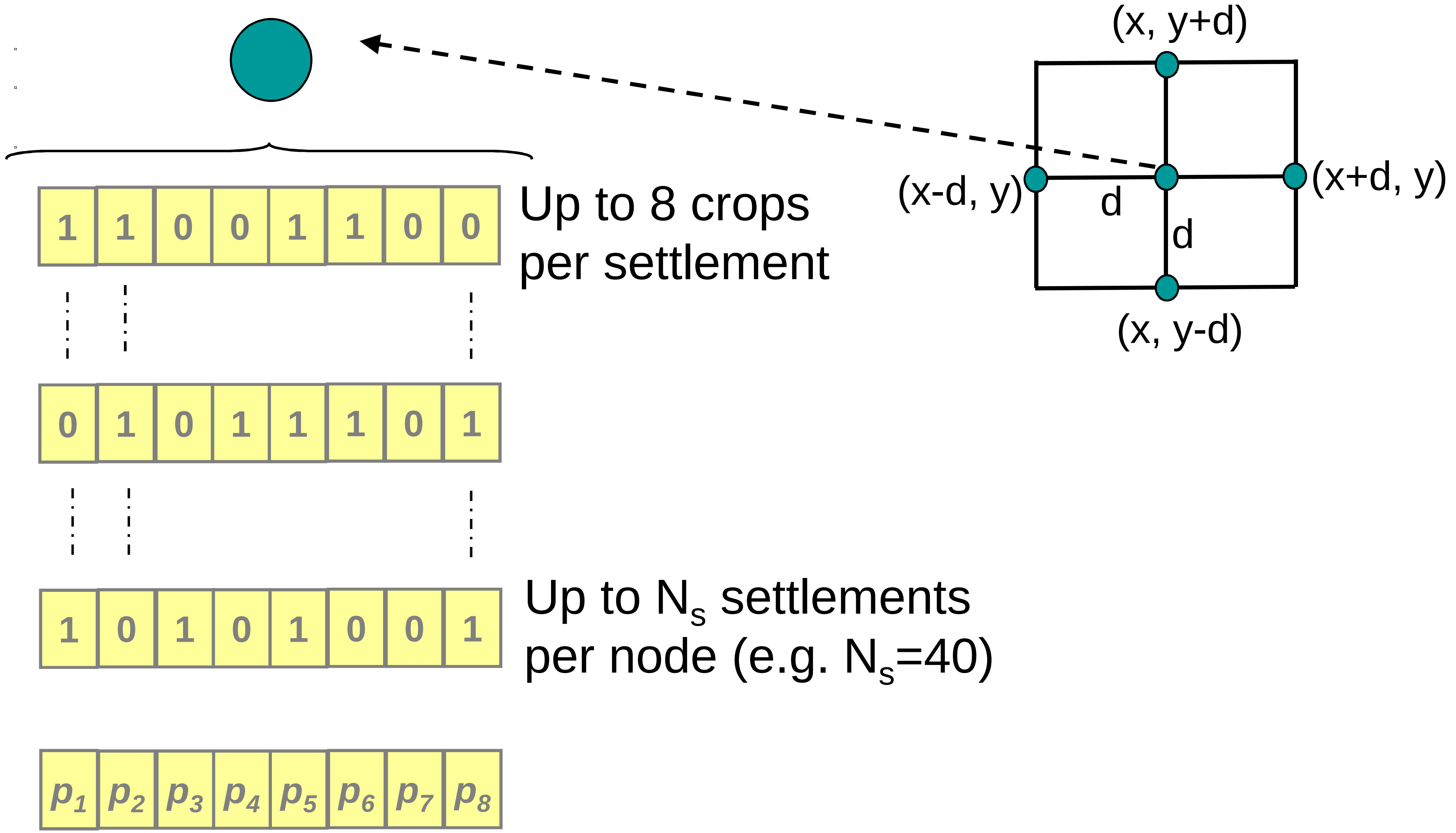


$P(t)$ = population density

p_e = persistency

Ro = reproductive rate (net fecundity)

Initial crops from pre-LBK frequencies at the central node

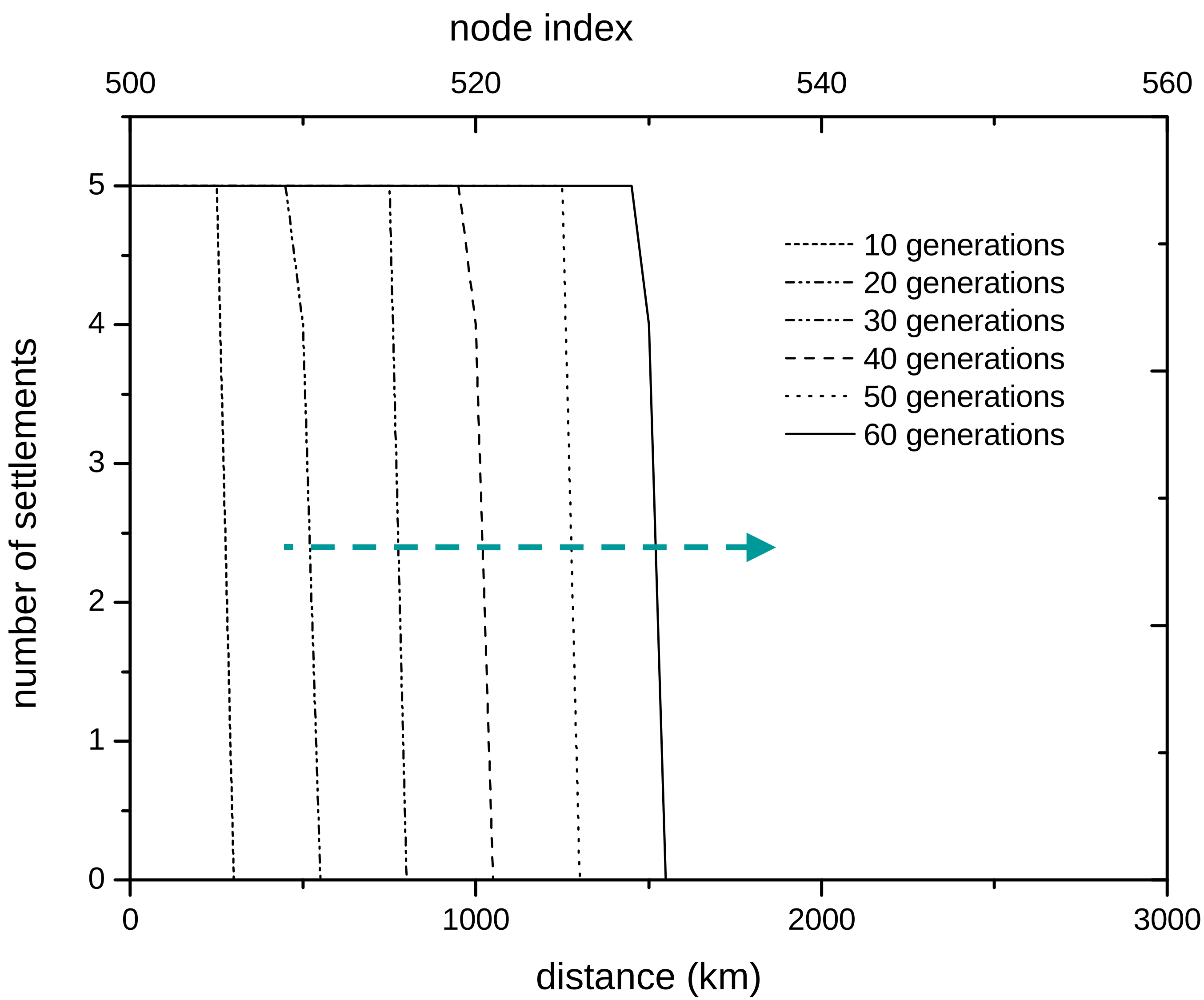


Model parameters

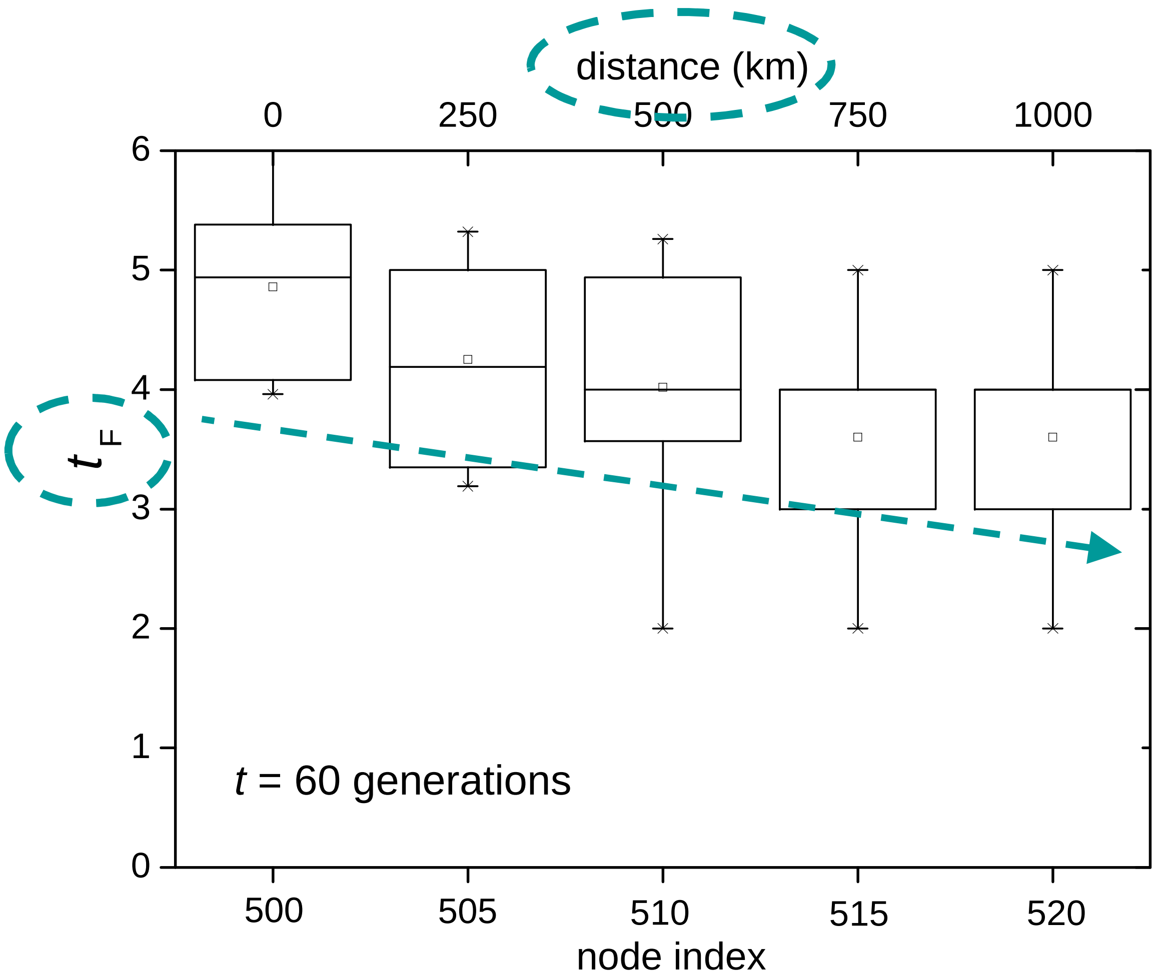
symbol	name	value	units	Ref.
p_e	persistence	0.38	--	Stauder (1971)
Ro	reproductive rate*	1.4	--	Conolly et al. (2008)
	generation time	32	yr	Stauder (1971)
d	grid distance	50	km	Stauder (1971)
Ns	maximum number of settlements per node	5-40	--	Zimmerman et al. (2009)
t	final time	60	gen	Conolly et al. (2008)

New settlements are identical to their ‘parents’ → no horizontal transmission is applied → demic model

Simulated demic front of LBK settlements



Cultural Diversity as a Function of Distance



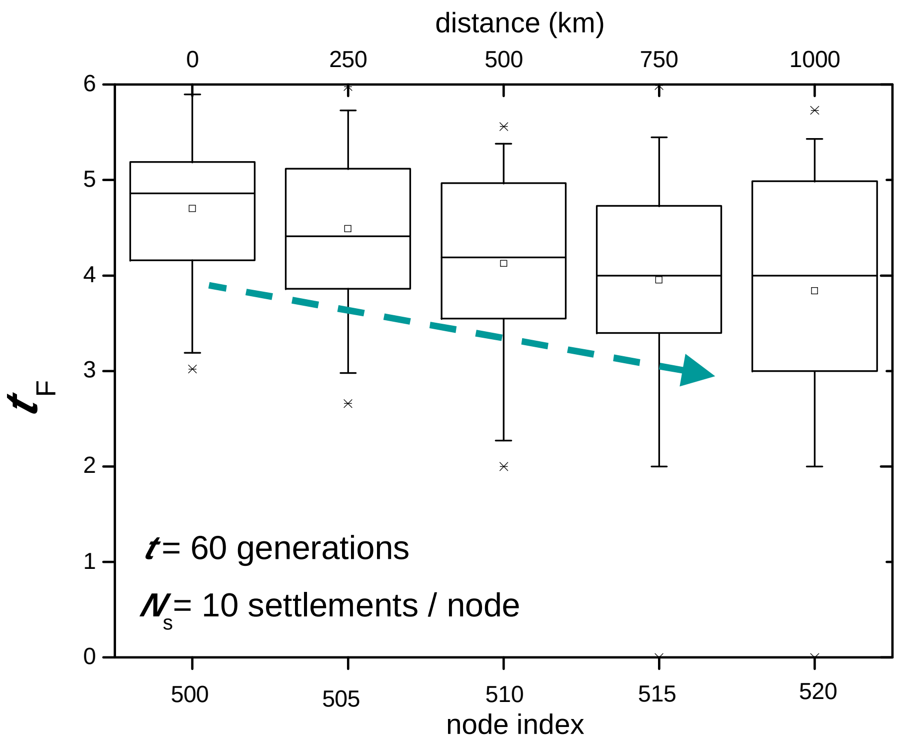
Recall:

Final observed

t_F=3.7

Boxplot of 20 simulations.

Similar decrease for other values of Ns

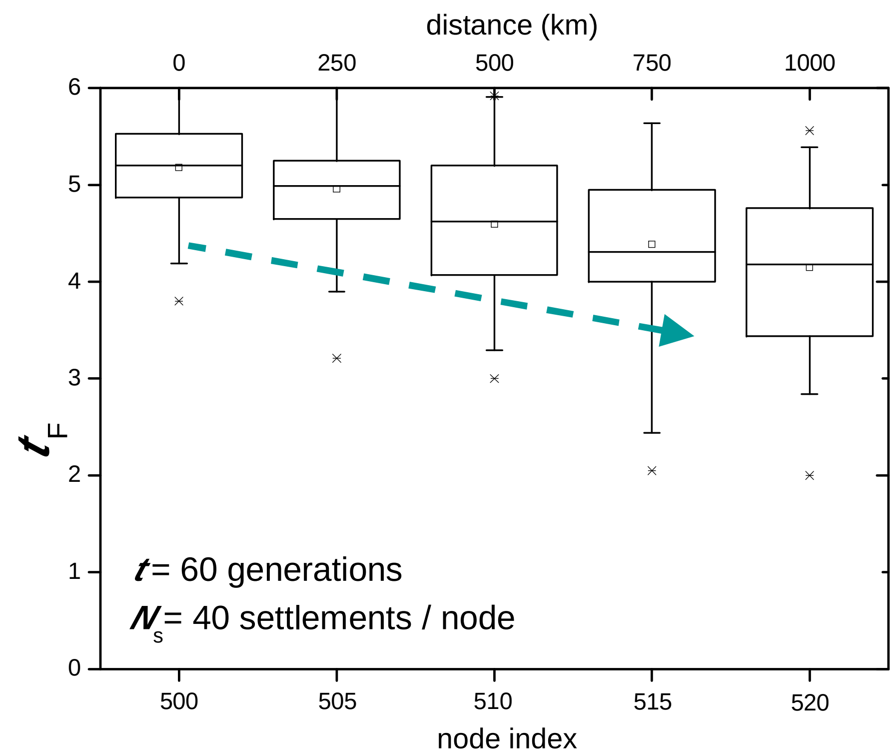


Pérez-Losada & Fort
J. Arch. Sci. (2011)

Recall:

Final observed

t_F=3.7



Questions?