

Neolítico en el Mediterráneo: Velocidad, efecto cultural, genética, mezcla de poblaciones

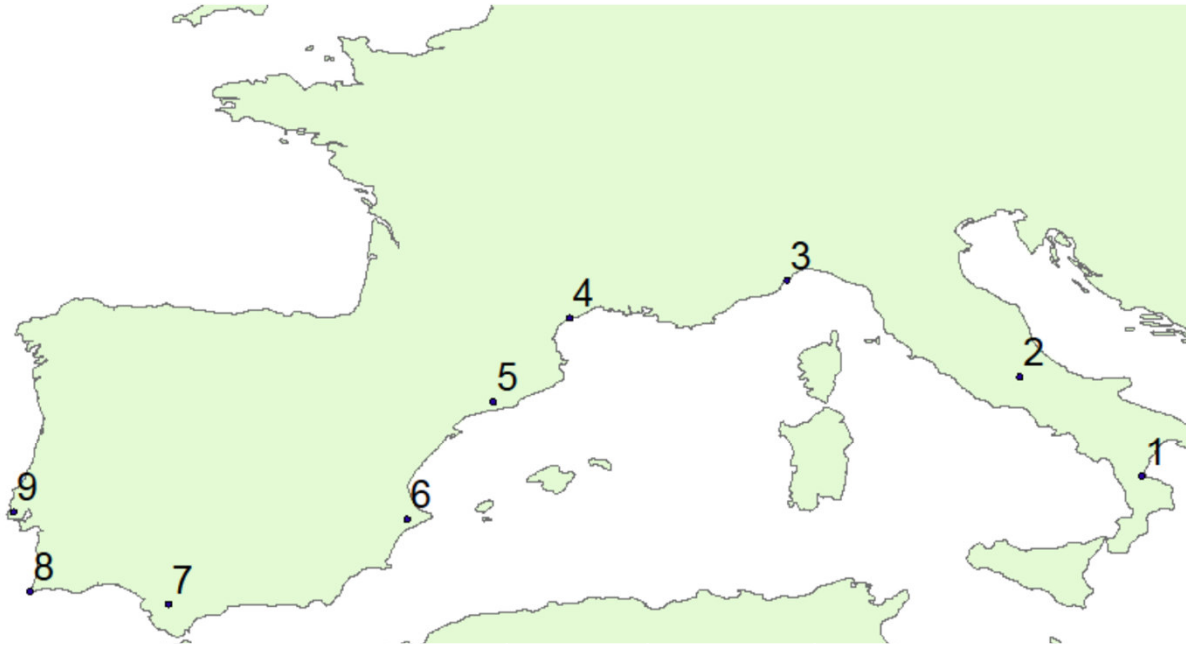
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Universitat de Girona
3^r seminario Neonet
Madrid, 26 Abril 2024



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Background

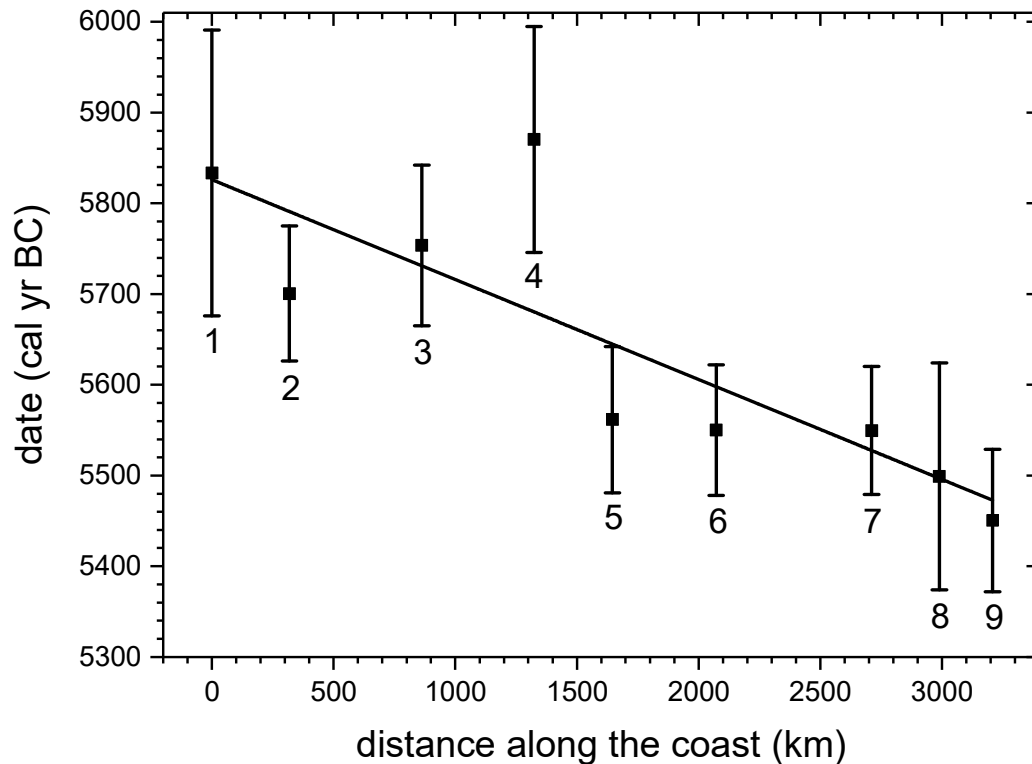
- 20 years ago Zilhao (*PNAS* 2001) noted that **'the dates for the first appearance of the Neolithic package are indistinguishable statistically from central Italy to Portugal'**. He reached this conclusion after rejecting almost all dates, e.g., all long-lived samples (due to the old-wood effect).
- 15 years ago it was still not possible to estimate the spread rate in km/yr due to the paucity of reliable dates (Zilhao, personal communication, 10/3/2006).
- 5 years ago we estimated the spread rate as **8.7 km/yr** (Isern, Zilhao, Fort & Ammeran, *PNAS* 2017).
- This year: analysis on dispersal distances and the cultural effect (Fort, AAS 2022). It is the topic of this talk.



- New database.
- 215 early Neolithic sites.
- 3 new regions: 1, 2, and 4 (not included in our *PNAS* 2017).
- Oldest date per region on a domesticated, short-lived species.

Region	uncal BP	error	cal. BC max	cal. BC min	site
1 Southwestern Italy	<u>6956</u>	75	5991	5676	<u>Favella della Corte</u>
2 Central western Italy	6809	45	5774	5626	Colle Santo Stefano
3 NW Italy/SE France	6870	40	5842	5665	Arene Candide
4 Languedoc/Roussillon	<u>7010</u>	60	5995	5746	<u>Pont de Roque-Haute</u>
5 Catalonia	6655	45	5642	5481	Guixeres (de Vilobí)
6 Valencia	6600	50	5622	5478	Mas d'Is
7 Andalusia	6609	35	5620	5479	Dehesilla
8 southern Portugal	6550	70	5624	5374	Cabranosa
9 central Portugal	6497	34	5529	5372	Lameiras

Spread rate



9.1 km/yr, $r = 0.84$.

It is encouraging that this spread rate is similar to our previous estimation of 8.7 km/yr (Isern et al., *PNAS* 2017).

Bootstrap resampling using the calibrated probability distribution for each site: **7.5-10.6 km/yr** (80% CL). We will use this range in other slides. The mean is 9.1 km/yr, nicely consistent with the value above.

Technical note: The usual approach (based Student's t) yields 5.9-12.3 km/yr (80% CL) but is invalid because the data (squares) have not been found by sampling₄ from normal distributions with a single variance and centered about the regression.

Models and simulations

- Rectangular grid of square cells. This allows us to obtain analytical equations for the spread rate.

A real map would yield similar results (Isern et al., *PNAS* 2017).

- Initially farmers only at the lower row.
- 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 (of 1 generation =32 yr), we compute 3 processes:

(1) Reproduction: logistic, with net fecundities $R_0 = e^{aT} = 2.45$ for farmers and $R'_0 = e^{a'T} = 1.81$ for HGs (from ethnographic data), where a and a' are the growth rates.

Technical note: Carrying capacities: 1.28 farmers/km², 0.064 HGs/km² (from ethnography). They do not have any effect on the spread rates, neither does R'_0 .

Simulations

(2) Cultural transmission (e.g., interbreeding):

P_N = farmers

P_{HG} = hunter-gatherers

Cultural transmission theory [1-3] (children of mixed matings are farmers):

$$P_N(t + 1, x, y) = P_N(t, x, y) + \eta \frac{P_{HG}P_N}{P_{HG} + P_N}$$

$$P_{HG}(t + 1, x, y) = P_{HG}(t, x, y) - \eta \frac{P_{HG}P_N}{P_{HG} + P_N}$$

η = intensity of interbreeding $0 \leq \eta \leq 1$ (random mating $\rightarrow \eta = 1$)

[1] Cavalli-Sforza & Feldman, *Cultural transmission & evol.*, Princeton 1981

[2] Fort, *Phys. Rev. E* 2011

[3] Fort, *PNAS* 2012

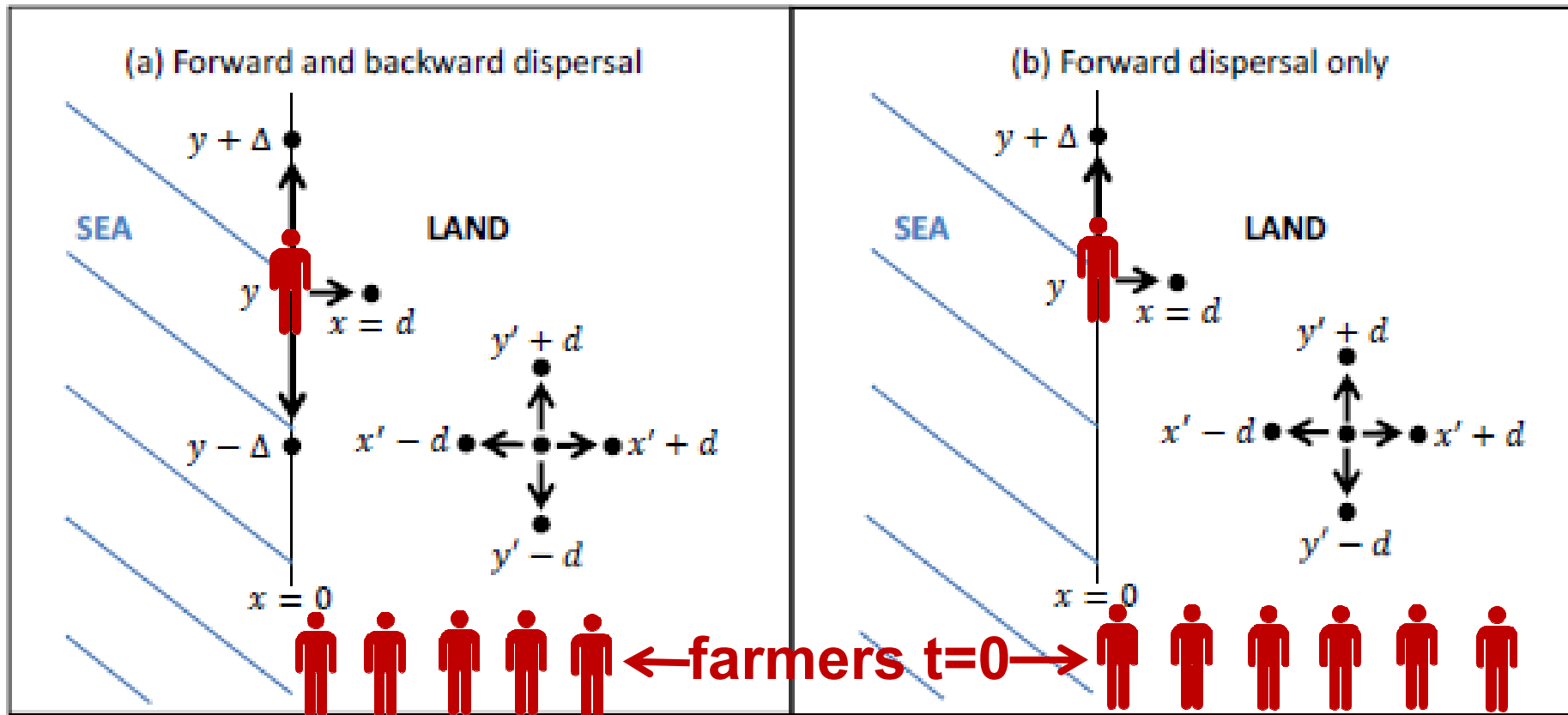
(3) Dispersal: 38% do not migrate ($p_e=0.38$), from ethnography.

Two dispersal ABMs: next slide

Two agent-based models (ABMs)

First model

Second model



Inland: $d = 50$ km from ethnography, and to obtain 1 km/yr as observed. We want to find what values of the sea-travel distance Δ are consistent with the observed spread rate along the coast (7.5-10.6 km/yr, slide #4).

Theory

First equations for the **spread rate s** along a coast [4]

· First model (forward and backward dispersal):

$$s = \min_{\lambda > 0} \frac{\ln \left[R_0^F (1 + \eta) \left(\frac{2p_e + 1}{3} + \frac{2}{3} (1 - p_e) \cosh(\lambda\Delta) \right) \right]}{\lambda T}$$

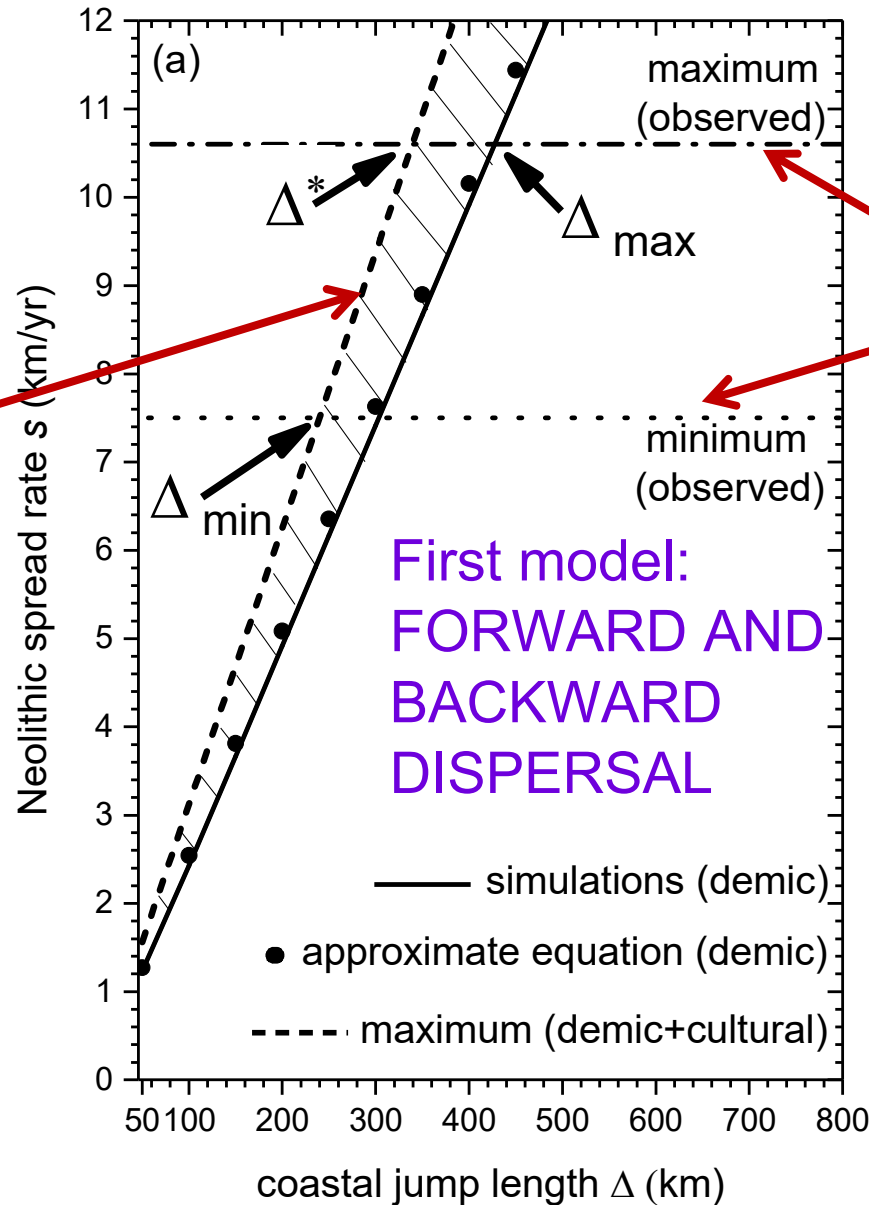
· Second model (forward dispersal only):

$$s = \min_{\lambda > 0} \frac{\ln \left[R_0^F (1 + \eta) \left(\frac{p_e + 1}{2} + \frac{1 - p_e}{2} e^{\lambda\Delta} \right) \right]}{\lambda T}$$

Results

maximum possible spread rate:

$$s_{max} = \Delta/T$$



archaeological data: 7.5-10.6 km/yr (slide #4)

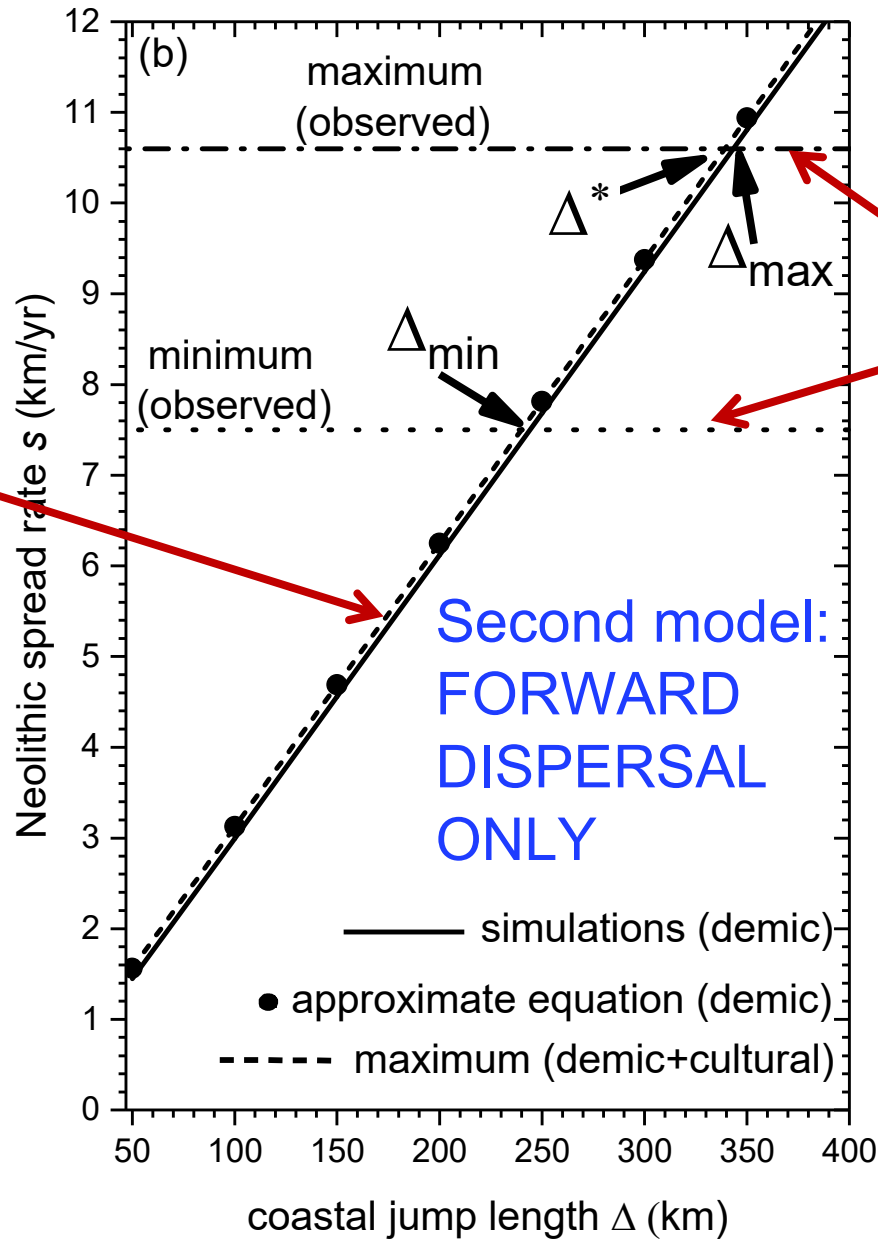
Results from this figure:

$$\Delta_{min} = 240 \text{ km}$$

$$\Delta_{max} = 427 \text{ km}$$

Results

maximum possible spread rate:
 $s_{max} = \Delta/T$



archaeological data: 7.5-10.6 km/yr (slide #4)

Results from this figure:
 $\Delta_{min} = 240$ km
 $\Delta_{max} = 343$ km

Results

1st model (forward and backward dispersal): $\Delta_{min} = 240$ km, $\Delta_{max} = 427$ km

2nd model (forward dispersal only): $\Delta_{min} = 240$ km, $\Delta_{max} = 343$ km

Overall range: $240 \text{ km} \leq \Delta \leq 427 \text{ km}$ per generation

Technical notes:

1. Why are they much longer than **inland (about 50 km)**?

Perhaps because by foot: $5 \text{ km/hour} \cdot 10 \text{ hours} = 50 \text{ km}$

but ancient boats (reconstructions): $19 \text{ km/h} \cdot 13 \text{ h} = 250 \text{ km}$.

2. Not surprising because ethnographic records of pre-industrial peoples used to sea travel display such long distances. Examples:

-Fiji to Samoa (**>700 km**) to get married since >300 years ago.

-XIX-century migrations from Nukuria to Mimigo (**1,100 km**), the Gilberts to the Solomons (**1,900 km**) and to Buka (**2,200 km**), etc.

-routine travels of **650-975 km** by pre-Columbian Caribbeans.

-Kula ring travels, near Papua New Guinea, early XXth century, **150 km**.

-Obsidian trade in near Oceania: **240 km** 20,000 yr BP, **400 km** by¹

Lapita populations 3,000 yr ago.

Cultural effect

Cultural effect= Percentage C of cultural diffusion [3]:

$$C = \frac{s - s_{\eta=0}}{s} \cdot 100 \quad (1)$$

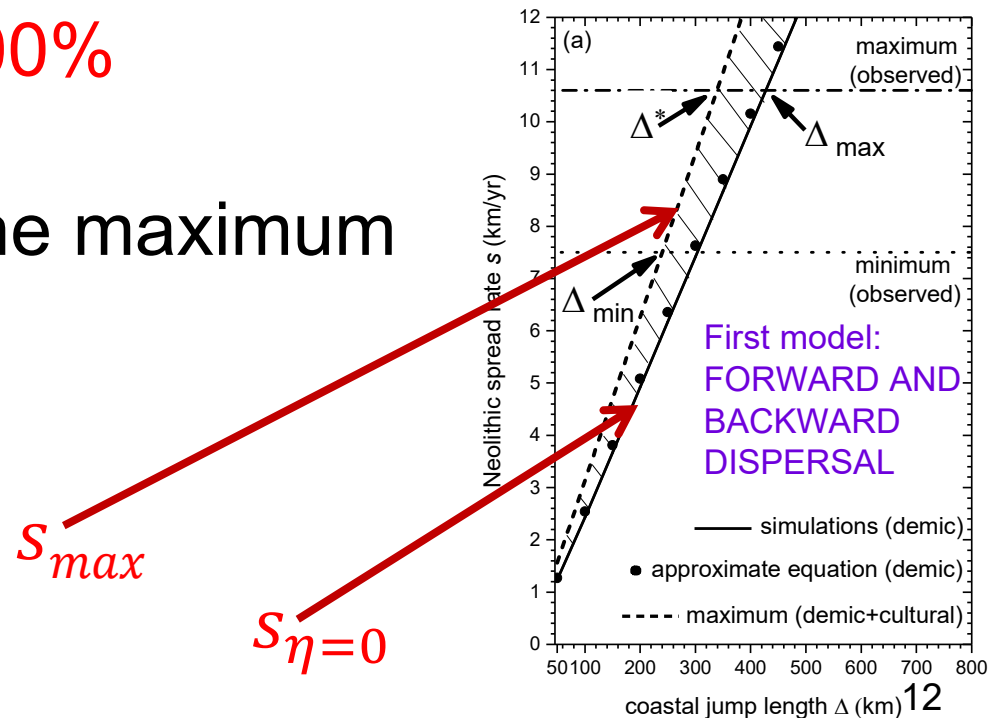
Percentage D of demic diffusion:

$$D = \frac{s_{\eta=0}}{s} \cdot 100$$

Therefore: $C + D = 100\%$

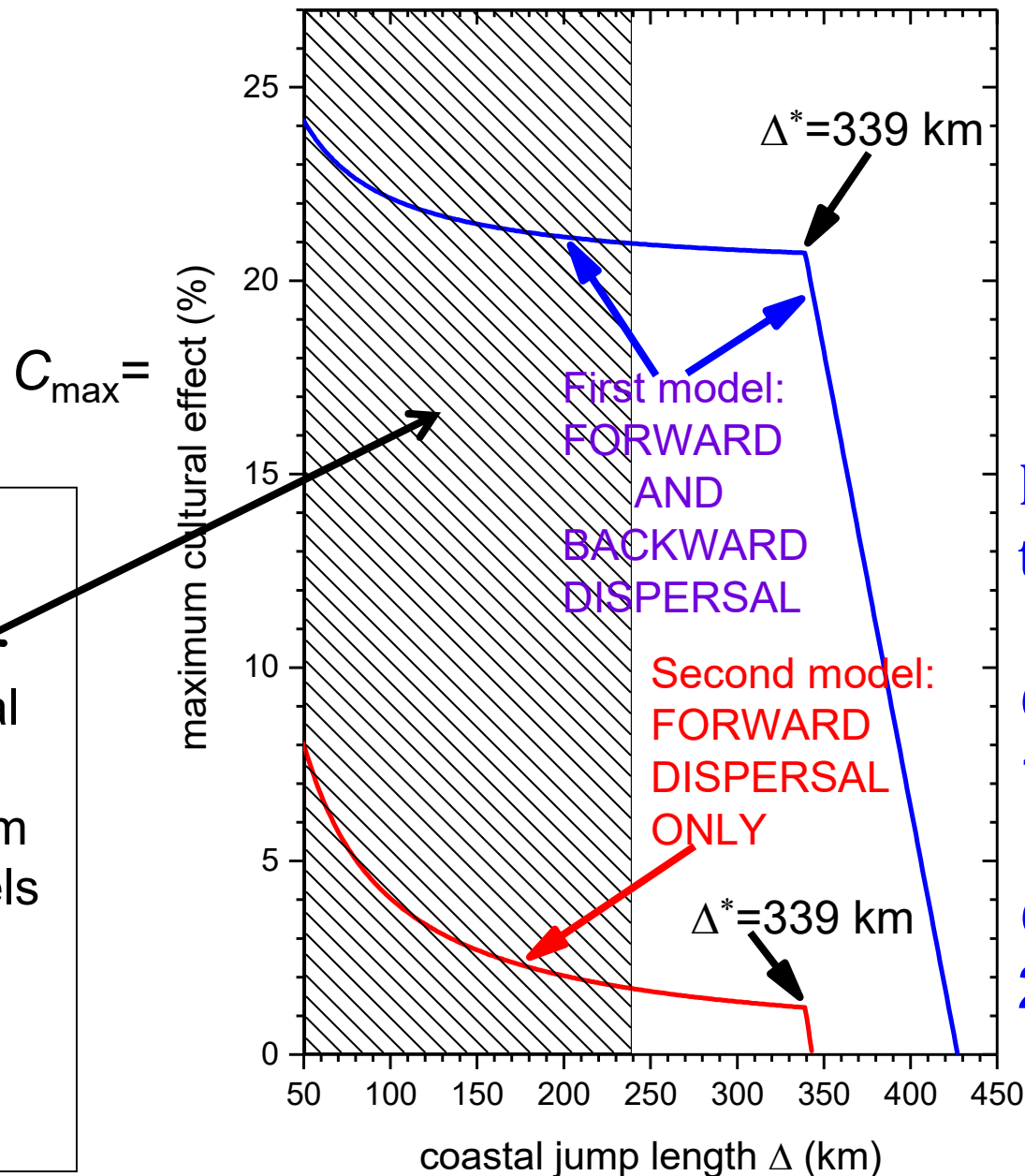
From Eq. (1) we find the maximum cultural effect:

$$C_{max} = \frac{s_{max} - s_{\eta=0}}{s_{max}} \cdot 100$$



Results

shaded area:
inconsistent
with the
archaeological
data because
 $\Delta_{min} = 240$ km
for both models
because
minimum
speed = 7.5
km/yr



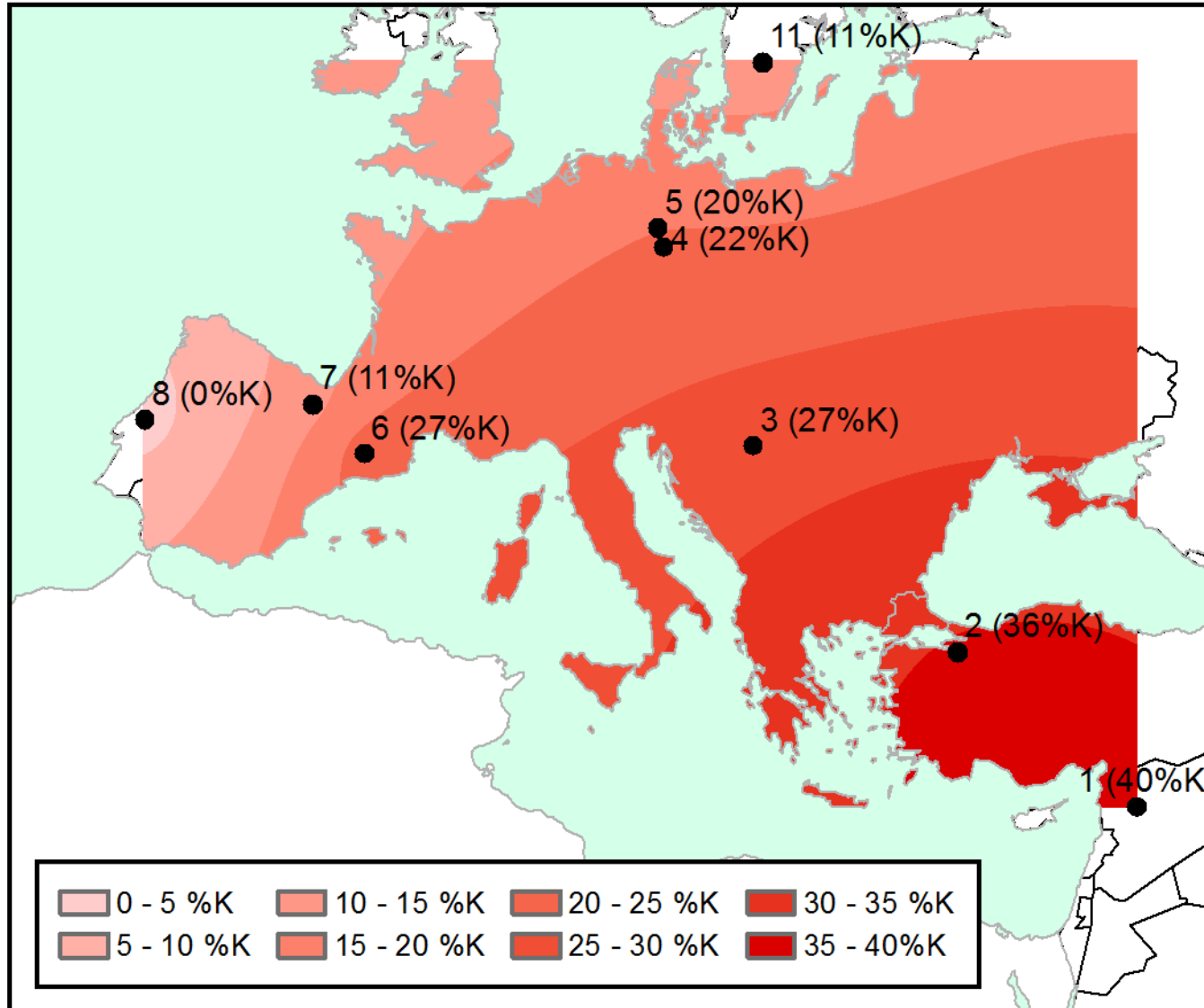
Results from
this figure:

$C_{max} = 0-21\%$
1st model

$C_{max} = 0-2\%$
2nd model

Ancient genetics

mtDNA haplogroup K: absent in hunter-gatherers



**This
pattern
(cline)
suggests
interbreeding**

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



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, from ethnography)
- (2) **Cultural transmission**: next slide.
- (3) **Reproduction**: next slide.



Simulations

(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).

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

Cultural transmission theory (Cavalli-Sforza & Feldman 1981;

Fort 2011, 2012): $\text{couples } HN = \eta \frac{P_{HG}P_N}{P_{HG} + P_N + P_X}$

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

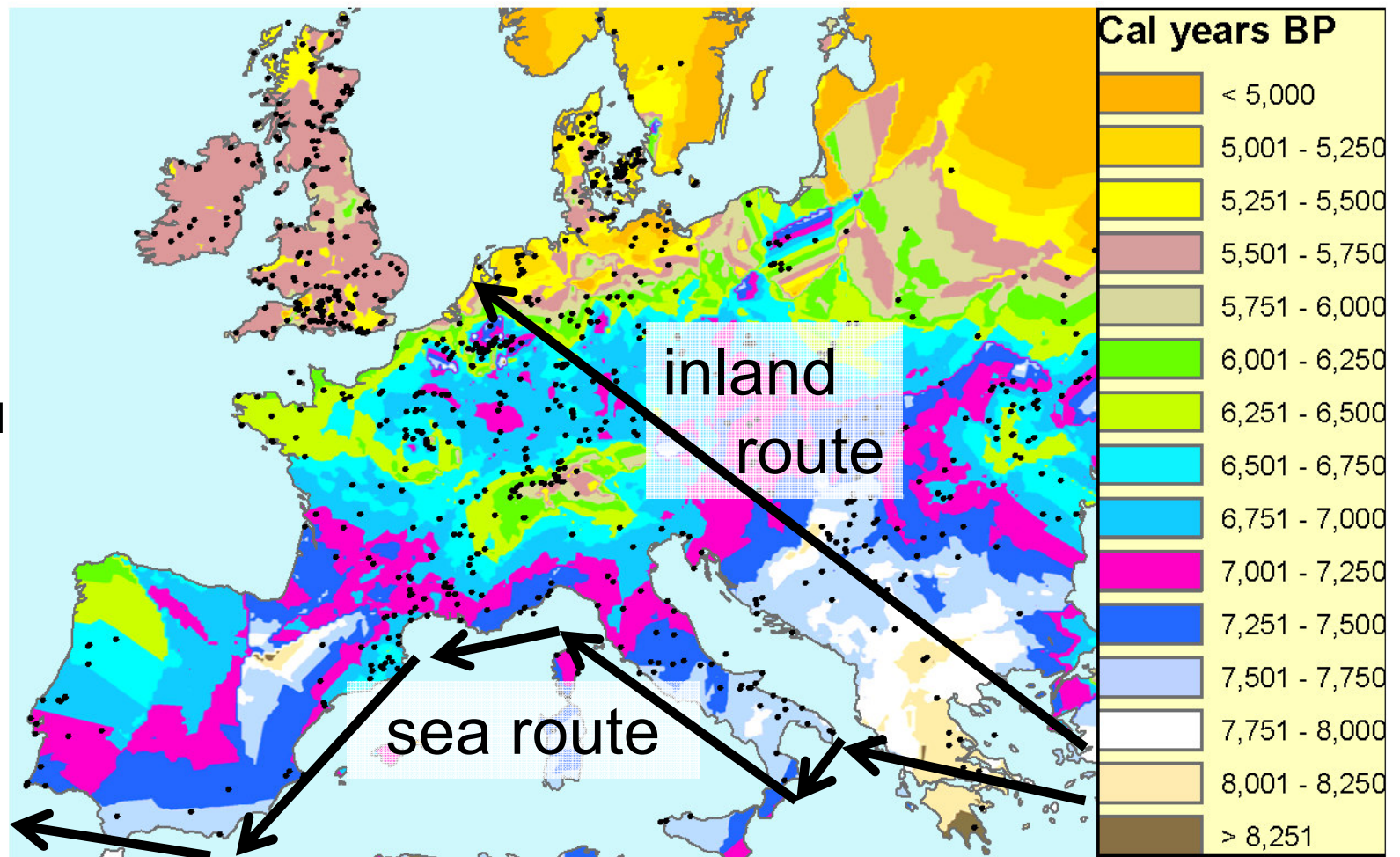
random mating for farmers \rightarrow $\text{couples } NX = \frac{P_N P_X}{P_N + P_X}$

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



Two routes

interpolation
of
archaeological
dates
from
Fort,
*J. R. Soc.
Interface*
(2015)

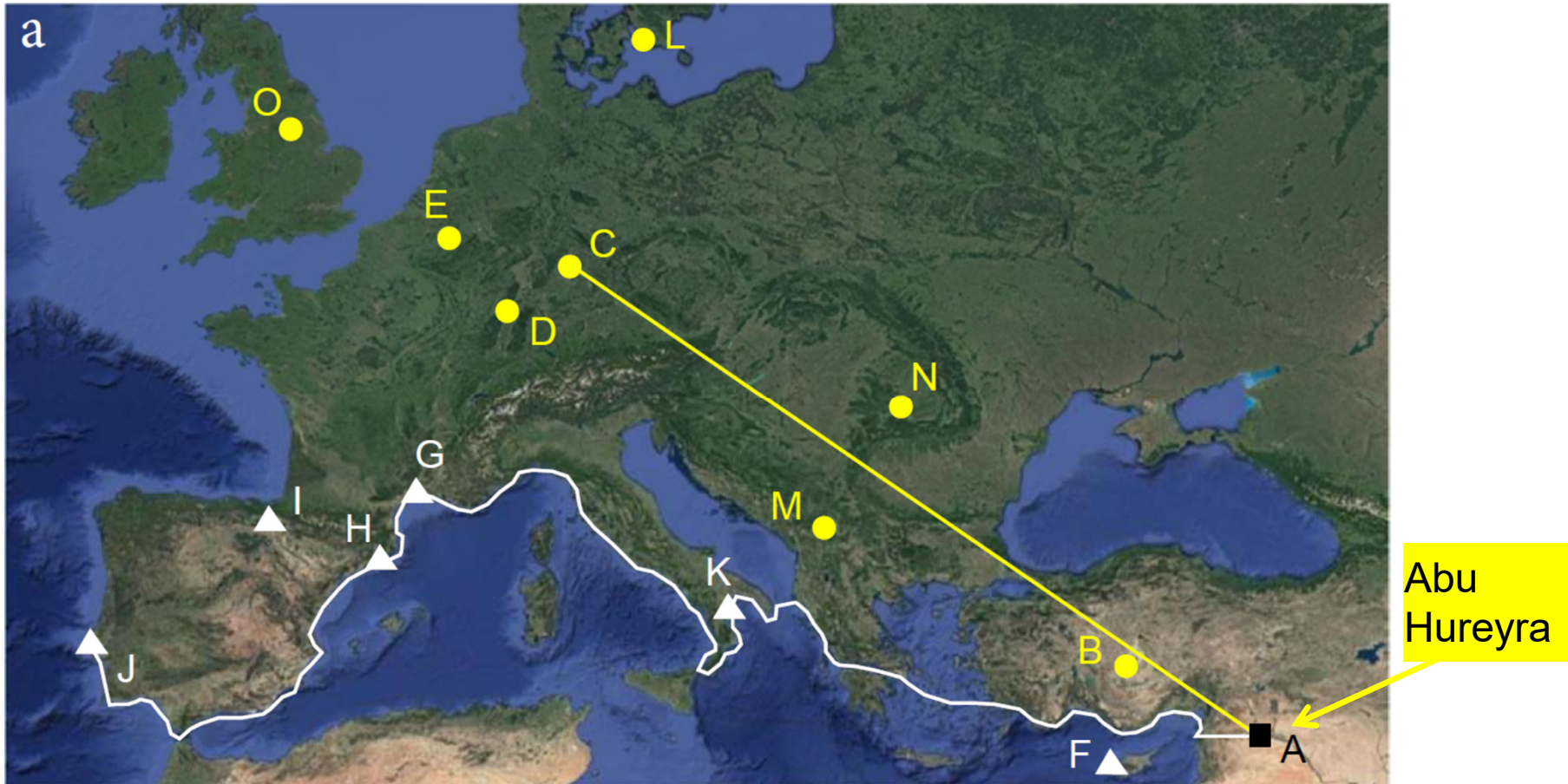


Now (year 2024) we have ancient genetic data for both routes



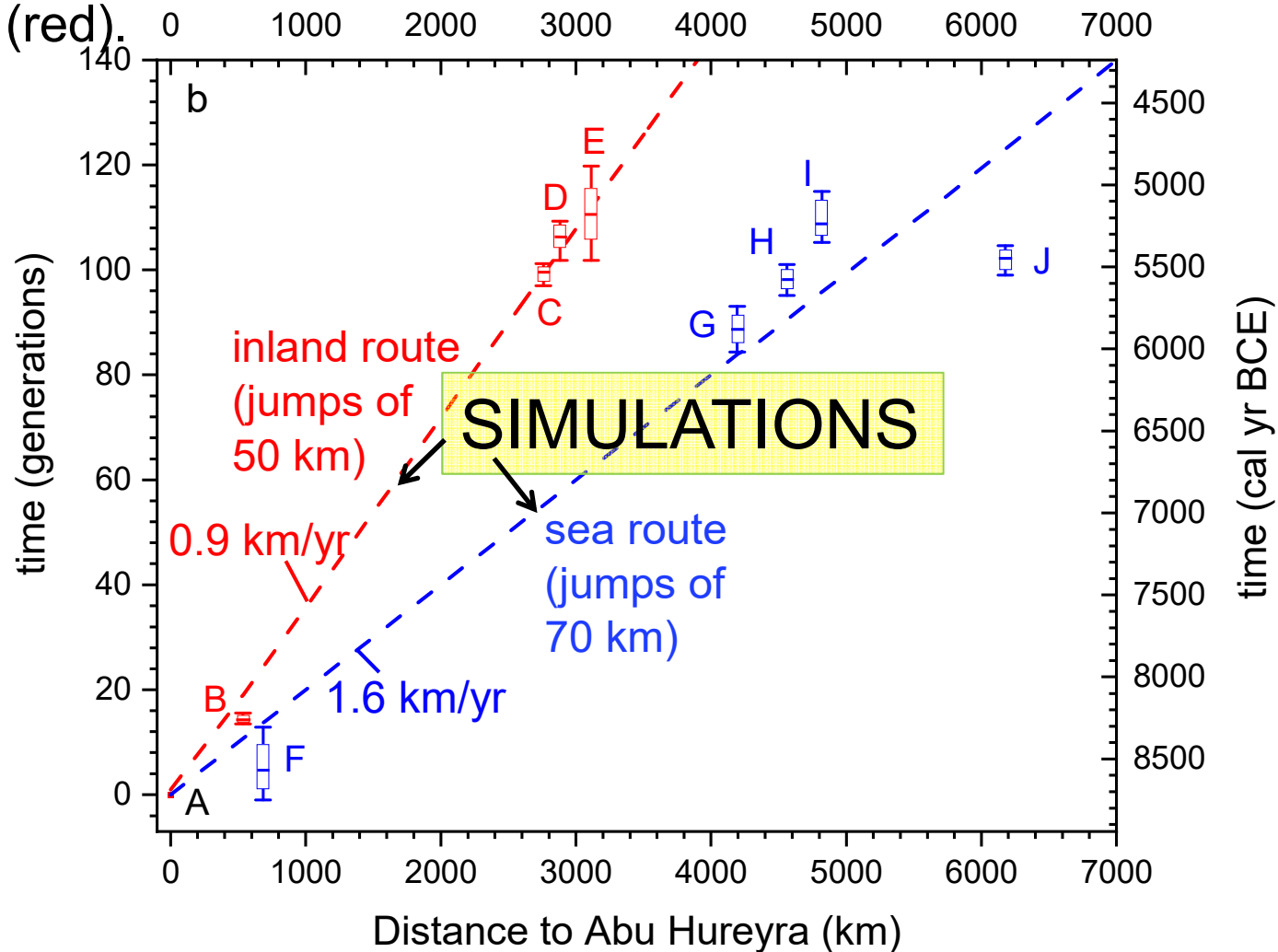
Distances

- (1) Inland route: great circles = 'straight lines'
- (2) Sea route: sea-see.com



Simulations + archaeological data

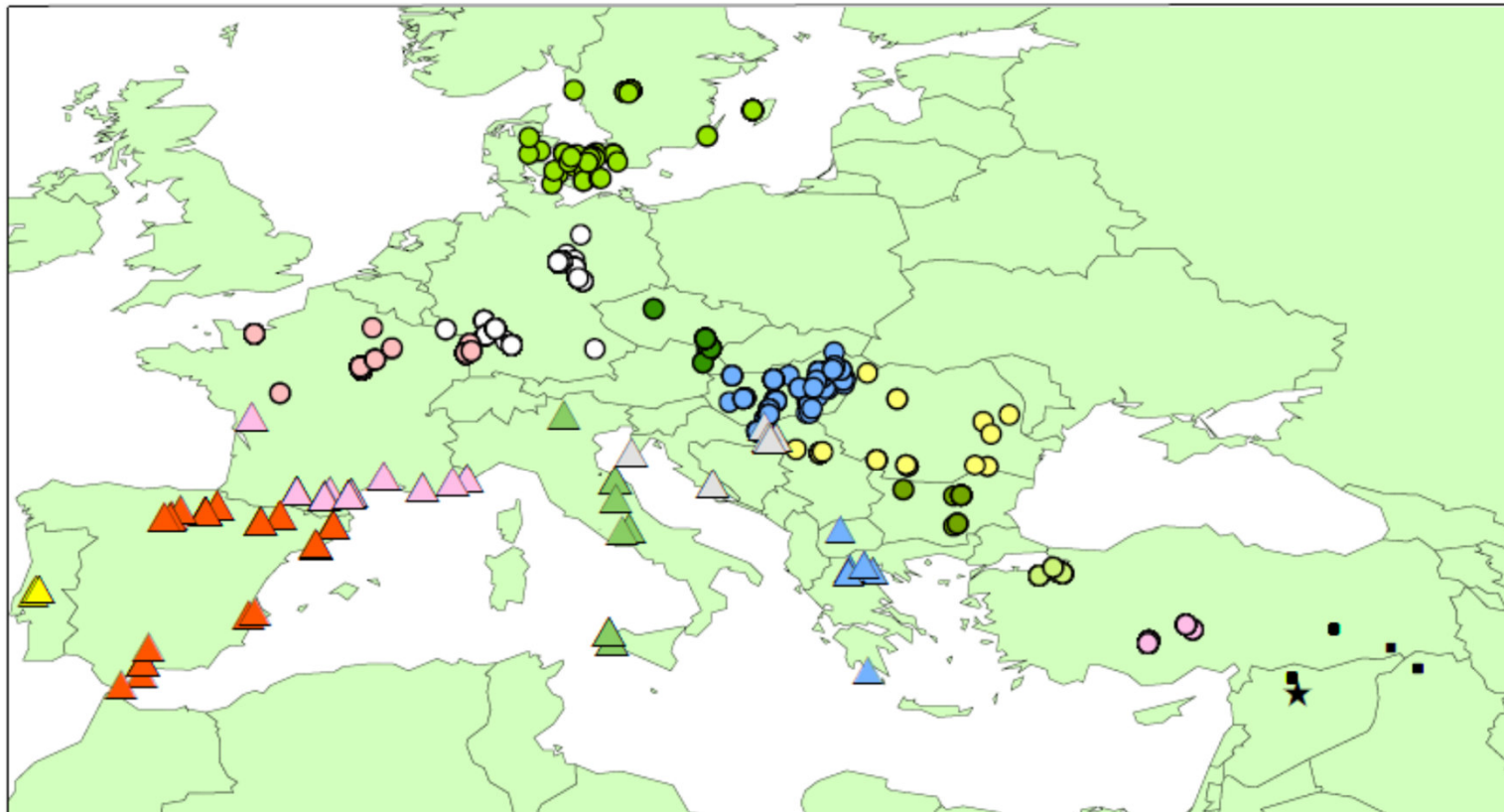
Initially there are farmers only at the cell with the **oldest PPNB site in Upper Mesopotamia (Abu Hureyra, <9,038 cal BC)** at a date (8,718 cal BC) such that the simulations agree with the data along the inland route (red).



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

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

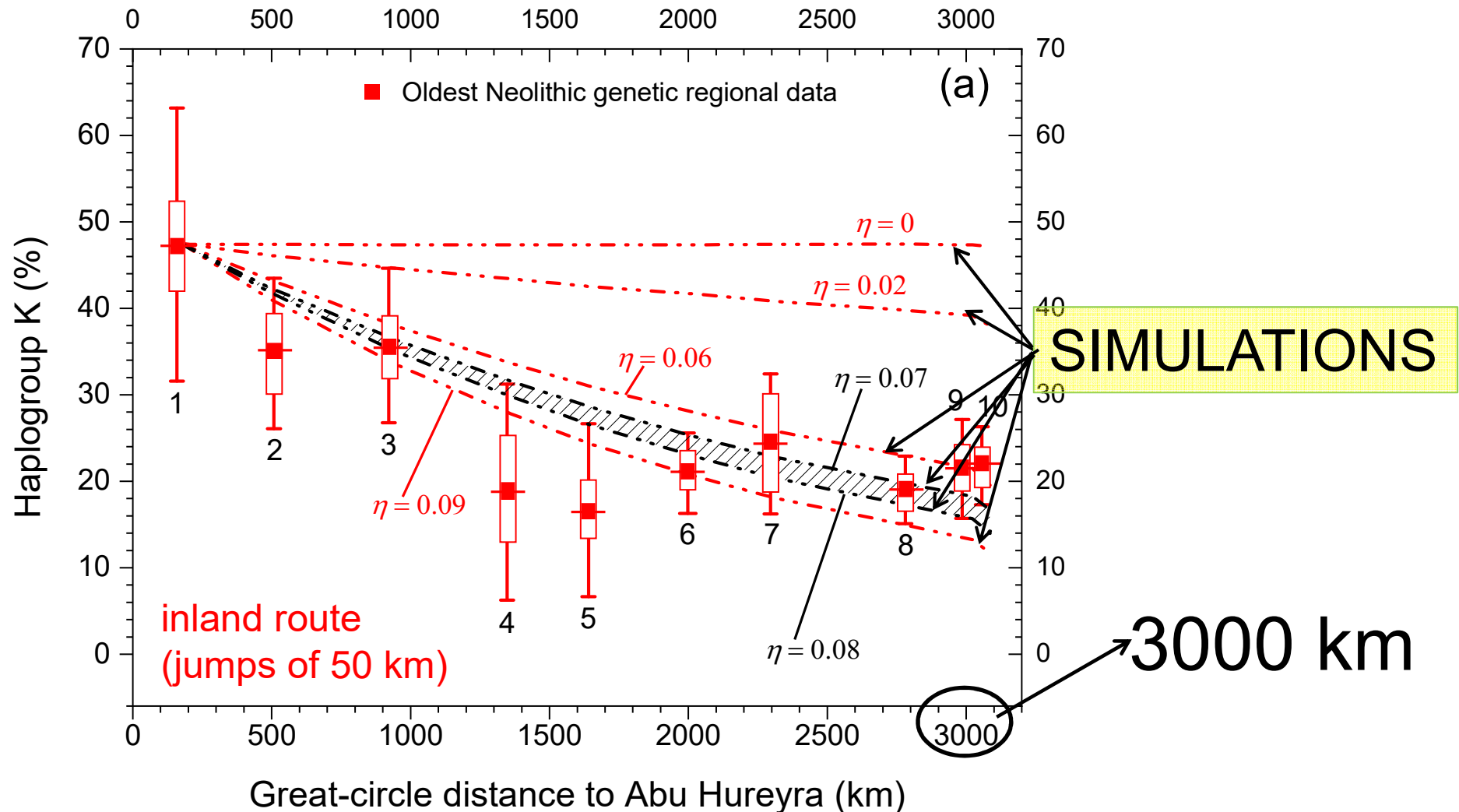




Sites with genetic data. Circles and triangles stand for inland and Mediterranean routes

- | | |
|---|------------------------------|
| ★ Abu Hureyra (oldest PPNB site in region 1, no genetic data) | ● 9 Scandinavia |
| ▪ 1 Northern Mesopotamia (presumed region of origin) | ○ 10 Northern France |
| ○ 2 Central Anatolia | ▲ 11 Greece and N. Macedonia |
| ○ 3 Western Anatolia | ▲ 12 Croatia |
| ● 4 Bulgaria (except Malak Preslavets) | ▲ 13 Italy |
| ● 5 Romania and Serbia (except Iron Gates) | ▲ 14 Southern France |
| ● 6 Hungary | ▲ 15 Spain |
| ● 7 Austria and Czech R. | ▲ 16 Portugal |
| ○ 8 Germany | |

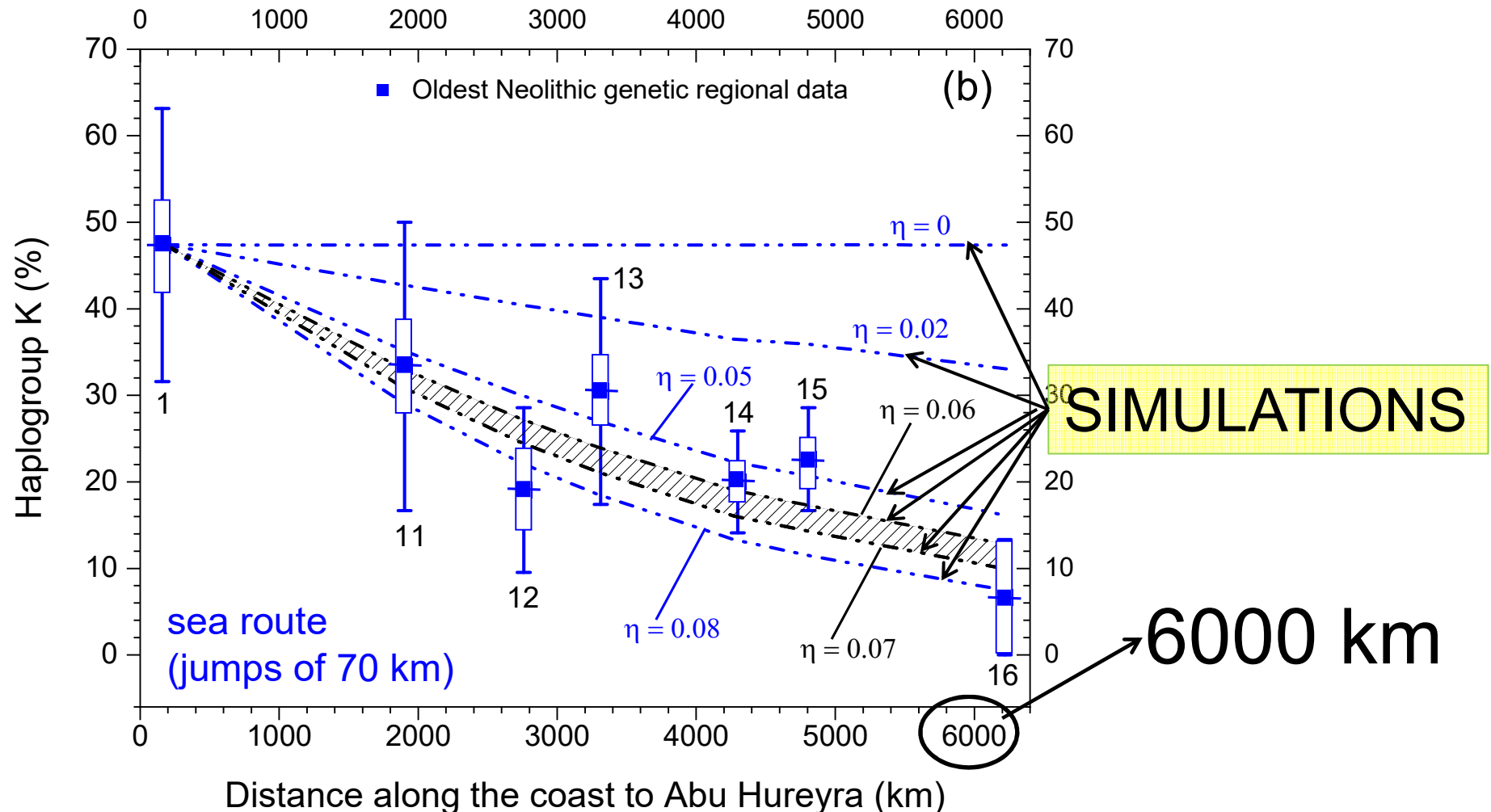
Inland genetic cline



Best fits: $\eta = 0.07-0.08$



Mediterranean genetic cline



Conclusions

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 interbreeding and/or acculturating fraction of farmers ($\eta = \mathbf{0.07}$ or about $\mathbf{3.6\%}$ * of farmers) was the same along both routes. **It did not depend on geography but only on the transition in the subsistence economy and its way of life.**

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



Posibles colaboraciones (Neonet)

1. Mediterráneo oriental: propagación mucho más lenta!
Necesitamos base de datos para estimar velocidad.
2. Norte de África: ¿continuación del Mediterráneo Occidental?
¿Coherente con la velocidad ya estimada?
3. Genética: el cromosoma Y da coherente con el ADN mitocondrial ($\eta = 0.07$). ¿Y el resto del genoma?
Hay datos suficientes para regiones de autosomas que (casi) no recombinen?
Hay alguna forma de extender nuestro modelo a datos del genoma completo?

